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Ecological assembly of high-diversity plant communities: dispersal, competition, and environmental filtering in longleaf pine savannas

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ECOLOGICAL ASSEMBLY OF HIGH-DIVERSITY PLANT COMMUNITIES: DISPERSAL, COMPETITION, AND ENVIRONMENTAL FILTERING IN LONGLEAF PINE SAVANNAS

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ABSTRACT

Ecological mechanisms proposed to explain community assembly and the maintenance of biodiversity are hypothesized to fall along a theoretical continuum bounded at one extreme by deterministic processes ("niche assembly") and at the other extreme by stochastic processes ("dispersal assembly"). In this dissertation, I explore the idea that the position of ecological communities along the niche-dispersal assembly continuum is dynamic in space and time. Using field experiments in a high-diversity longleaf pine savanna, I test the general hypothesis that "ecological filters" (competition, disturbance, and resource availability) contribute to niche assembly through their effects on established plant species and recruitment from the species pool. Consistent with dispersal-assembly theory, I found that dispersal from the species pool strongly limited local species diversity regardless of the presence of these three niche-based ecological filters. Importantly, however, some ecological filters (e.g., space limitation in communities with low-intensity fire disturbance and establishment limitation imposed by drought and high-rainfall conditions) limited the extent to which community assembly was influenced by dispersal, suggesting ecological conditions that reduce stochastic community assembly in high-diversity communities.

I examined the generality of these patterns by conducting a meta-analysis of >60 published experiments. I found that dispersal strongly limited species richness in a wide range of plant communities, but that dispersal had a stronger positive effect on species richness in more disturbed communities and when the species pool contained high species diversity and functional-trait diversity, supporting the hypothesis that community assembly reflects a dynamic interplay between species-pool diversity and local environmental heterogeneity.

My results suggest a conceptual model for community assembly in high-diversity pine savannas, with implications for other species-rich plant communities. I propose that

characteristics of high-diversity communities (large species pools and pervasive recruitment limitation in populations of many rare species) generally contribute to stochastic community assembly, but that niche-based ecological filtering of resident species and immigrating species can shift high-diversity communities towards more deterministic community assembly. This conceptual framework has broader implications for understanding the maintenance of biodiversity and species coexistence in communities of contrasting diversity and for conserving biodiversity in longleaf pine communities threatened by habitat loss, fragmentation, and environmental change.

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CHAPTER 1. INTRODUCTION

Variation in species diversity is one of the most striking patterns in the natural world. Species richness, relative abundance, and composition vary dramatically at local, regional, and global spatial scales (Huston 1994; Rosenzweig 1995). These patterns have challenged biologists to explain the evolutionary and ecological processes involved in both the origin and maintenance of biodiversity (Ricklefs and Schluter 1993), and not surprisingly, there is no shortage of hypotheses to explain patterns of species diversity and coexistence (e.g., Palmer 1994 identified at least 120 plausible hypothese proposed to explain variation in species richness). The vast number of mechanisms hypothesized to structure species diversity has recently inspired the development of synthetic theories in ecology that organize some of this complexity into more general conceptual frameworks, but in general, theoretical advancements continue to outpace empirical tests of key model predictions (Agrawal et al. 2007). Consequently, major gaps remain in our mechanistic empirical understanding of biodiversity patterns (e.g., Silvertown 2005), and therefore in our ability to conserve biodiversity and the ecosystem services it provides (e.g., Ehrlich and Wilson 1991).

In this dissertation, I draw on prominent theoretical models in community ecology to develop and test hypotheses on community assembly, the maintenance of species diversity, and species coexistence in plant communities. In this chapter, I first introduce the general conceptual framework that has motivated my research. The aim of this section is to provide an expanded introduction to the theoretical concepts and models that unify Chapters 2–4. Second, I introduce longleaf pine savannas and explain how they provide an ideal setting for understanding the ecological assembly of high-diversity plant communities. Finally, I conclude this chapter by providing an overview of the remaining chapters.

A SYNTHETIC CONCEPTUAL FRAMEWORK FOR COMMUNITY ASSEMBLY

Community ecology is currently in a period of rapid synthesis, with an increased emphasis on integrating local processes with regional processes to understand patterns and dynamics of biodiversity (Chapter 2; Leibold et al. 2004; Ricklefs 2004; Vellend in press). Local ecological processes, including biotic interactions among species and their responses to abiotic environmental conditions, form the cornerstone of classical models of species coexistence and diversity (Connell 1978; Tilman and Pacala 1993; Chesson 2000; Chase and Leibold 2003). Central to this "local" or "interspecific-interaction" perspective (Tilman 1997) on community diversity is the concept of the ecological niche, defined as "the joint description of the environmental conditions that allow a species to satisfy its minimum requirements so that the birth rate of a local population is equal to or greater than its death rate along with the set of per capita effects of that species on these environmental conditions" (Chase and Leibold 2003). Under this perspective, local biodiversity predominantly reflects the outcome of deterministic, niche-based species interactions including interspecific competition, predation, and facilitation. In contrast, the "regional perspective" emphasizes the importance of the regional species pool in the assembly of local communities (Tilman 1997). Under this perspective, the size of the regional species pool, history of colonization, and the rate of immigration into communities largely determine local biodiversity. The relative importance of local and regional processes in shaping biodiversity patterns continues to fuel insightful debate and synthesis in ecology (Ricklefs 1987; Harrison and Cornell 2008).

The local and regional perspectives can be organized along a theoretical continuum bounded at one extreme by niche-assembly theory and at the other extreme by dispersal-assembly theory (Hubbell 2001; Bell 2005; Gravel et al. 2006; Figure 1.1). Although each of these general theories embodies a large family of more detailed models and hypotheses (e.g.,

Chase and Leibold 2003; McGill et al. 2006), they provide general but contrasting predictions regarding the principal mechanisms involved in community assembly (Figure 1.1). Here, I focus on predictions regarding local species richness and community composition.

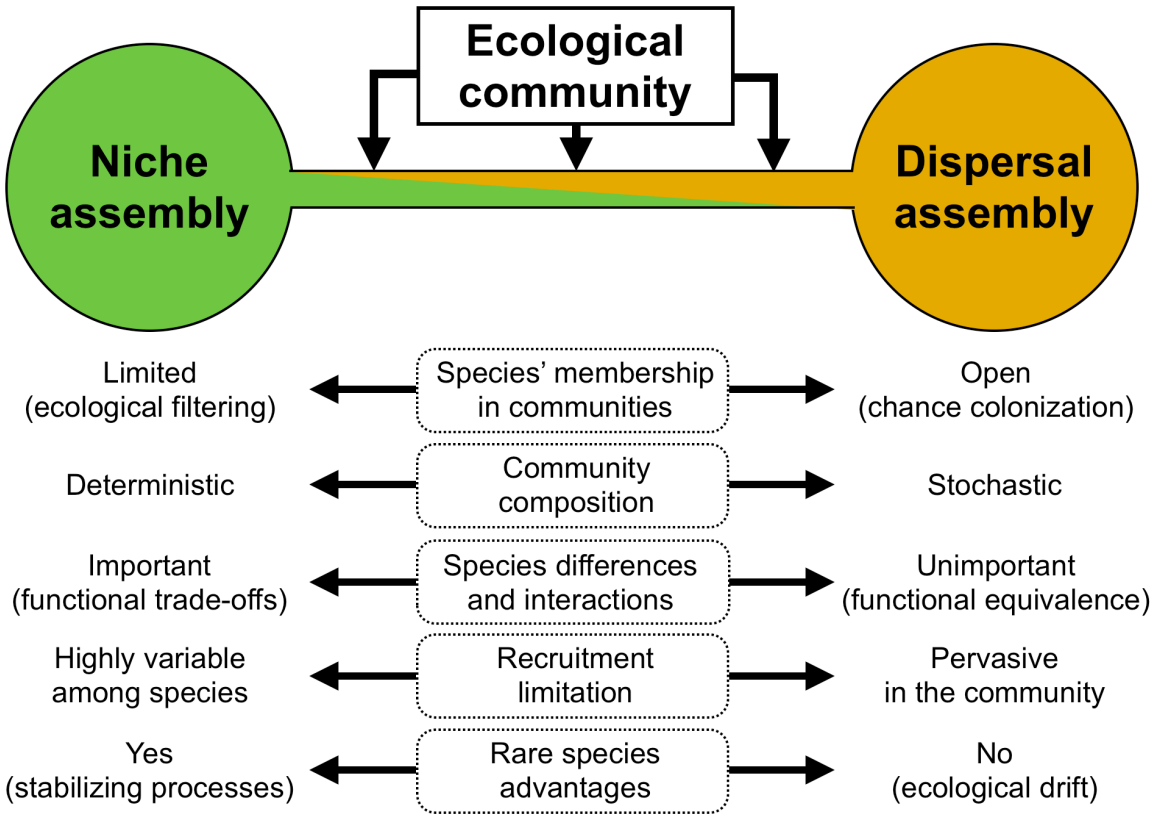

Figure 1.1. Community-assembly theory can be organized along a continuum bounded at one end by deterministic niche-assembly theory and at the other end by stochastic dispersal-assembly theory. An ecological community can be envisaged as falling anywhere along this continuum in space or time, depending on the presence and relative importance of mechanisms involved in community assembly. Note that not all of these mechanisms need to operate simultaneously at any given point on the continuum.

Dispersal-assembly theory, popularized in large part by Hubbell's (2001) Unified Neutral Theory of Biodiversity and Biogeography, proposes that chance colonization, rates of immigration from the species pool, pervasive recruitment limitation, and/or stochastic births and deaths are the primary ecological mechanisms influencing community assembly (MacArthur and Wilson 1967; Sale 1977; van der Maarel and Sykes 1993; Bell 2000; Hubbell 2001). Hubbell's

neutral theory represents an extreme version of the dispersal-assembly perspective, because it assumes that all species within guilds are equivalent with respect to their *per capita* probabilities of birth, death, and colonization, resulting in communities of "functionally equivalent" species whose abundances change randomly through time ("ecological drift"). Accordingly, local diversity is controlled by the size of the species pool (or metacommunity) and the rate of immigration. Dispersal-assembly theory makes at least two important predictions about the species richness and composition of local communities. First, local communities should be relatively "open-membership" assemblages (Hubbell 2001), i.e., communities open to invasion by most if not all species in the species pool. Consequently, local species richness should be positively related to the rate of immigration (i.e., dispersal) from the species pool (e.g., Chase et al. 2005). Second, local communities with similar environmental conditions should have dissimilar species composition, reflecting stochastic colonization and/or priority effects leading to multiple stable equilibria (Chase 2003, 2007).

Niche-assembly theory, in contrast, proposes that membership in local communities is controlled by biotic and abiotic conditions that deterministically limit local species membership (Chesson 2000; Chase and Leibold 2003, Figure 1.1). Here, each local community comprises species that possess traits required to establish and persist in the face of biotic and abiotic "ecological filters" that constrain membership from the species pool (Keddy 1992; Diaz et al. 1998). This theory makes at least two fundamental predictions. First, local communities should be "limited-membership assemblages" (Hubbell 2001), whereby local species richness either saturates or declines as the rate of immigration increases. Saturation occurs when species that arrive to local communities cannot attain membership owing to biotic and abiotic conditions (Elton 1958), whereas a decline in local diversity is predicted when immigration introduces dominant competitors or predators into local communities (Mouquet and Loreau 2003). Second,

local communities with similar environmental conditions are predicted to have similar species composition owing to deterministic filtering of the species pool during community assembly (Chase 2003, 2007). In addition, longer-term coexistence of species is hypothesized to result from processes that reduce negative interspecific interactions (stabilizing processes that allow species to increase in abundance when rare) and/or processes that minimize fitness differences between species (equalizing processes) (Chesson 2000; Adler et al. 2007).

Recruitment limitation is a key ingredient in both niche- and dispersal-assembly theory, but its mechanistic role differs between the two theories. Recruitment limitation is defined as the failure to recruit at a given site (Nathan and Muller-Landau 2000). This can result from both the failure of propagules to arrive ("seed limitation" or "seed arrival" in plants) and unsuitable conditions for establishment ("establishment" or "microsite limitation") (Nathan and Muller-Landau 2000). Seed limitation can be further decomposed into "dispersal limitation" and "source" or "fecundity limitation" (Clark et al. 1998). In dispersal-assembly theory, recruitment limitation is often assumed pervasive within communities ("recruitment limitation as a rule;" Barot 2004): populations of most—if not all—species in the community are recruitment limited owing to seed limitation, establishment limitation, or a combination of both processes. A fundamental consequence of community wide recruitment limitation is that it slows deterministic competitive exclusion in communities, allowing inferior competitors to "win sites by forfeit" that superior competitors fail to reach (Hurtt and Pacala 1995). In niche-assembly models, in contrast, recruitment limitation differs among species in a deterministic way. A classic example is the competition-colonization trade-off model of species coexistence, whereby populations of competitively dominant species are more dispersal limited than populations of less competitive species (Tilman 1994). More recently, Muller-Landau (2010) proposed the tolerance-fecundity trade-off, whereby populations of large-seeded species with higher stress tolerance are more seed

limited than populations of small-seeded species with higher fecundity. Evidence of recruitment limitation alone therefore cannot be used to disentangle the relative importance of niche and dispersal assembly (Adler et al. 2007; Clark 2009), but evidence for pervasive recruitment limitation leaves open the possibility that both deterministic and stochastic processes contribute to community structure.

High-diversity plant communities have served a prominent role in theoretical and empirical studies of dispersal and niche assembly. Dispersal assembly is hypothesized to play a particularly important role in high-diversity communities that contain large numbers of rare species and a large potential species pool. Rarity can contribute to stochastic dispersal assembly by: increasing demographic stochasticity (Barot 2004); limiting pairwise species interactions, resulting in unpredictable neighbors and diffuse competition (Grubb 1986; Hubbell and Foster 1986); and increasing community wide recruitment limitation, thereby slowing deterministic competitive exclusion (Hurtt and Pacala 1995). Moreover, communities assembled from a large species pool are more likely to have dissimilar species composition than communities assembled from a small species pool because there are more species in the regional pool that can coexist in any given community, increasing the probability that stochasticity in immigration history and priority effects influence community composition (Chase 2003).

Empirical studies in species-rich tropical forests and European chalk grasslands provide evidence for strong recruitment limitation and unpredictability in the species identity of neighboring competitors (Grubb 1986; Hubbell and Foster 1986; van der Maarel and Sykes 1993; Hubbell et al. 1999; Zobel et al. 2000), and tropical forests have arguably been the most scrutinized ecosystem in the continued debate over niche and dispersal assembly in community ecology. To date, empirical studies in tropical forests provide evidence that niche assembly (Volkov et al. 2005; Wills et al. 2006; John et al. 2007), dispersal assembly (Volkov et al. 2003;

Condit et al. 2006), and a combination of the two processes (Tuomisto et al. 2003; Paine and Harms 2009) contribute to community structure. One of the more common approaches in forest ecology has been to fit mechanistic models to empirical species-abundance distributions (SADs) (McGill et al. 2006). However, this approach has been criticized because models including both niche- and dispersal-assembly mechanisms can adequately predict SADs in natural communities, and therefore this approach cannot disentangle these two general mechanisms (e.g., Chave et al. 2002). Mixed empirical results such as these have contributed to the development of "hybrid" models and approaches that integrate both niche- and dispersal-assembly mechanisms (Tilman 2004; Gravel et al. 2006; Chase 2007), but we still have a limited empirical understanding of the ecological conditions that influence the position of high-diversity communities along this theoretical continuum.

In this dissertation, I explore the idea that the position of ecological communities along the niche-dispersal assembly continuum is dynamic in space and time. I examine this idea in an extremely species-rich and relatively understudied ecosystem with a large regional species pool and large numbers of rare species, i.e., under conditions in which we would expect stochastic processes to play at least some role in community assembly. I test the overarching hypothesis that three general ecological filters (interspecific competition, disturbance, resource availability) may shift the position of communities along this continuum towards niche assembly through their effects on both established plant species and recruitment of immigrants from the species pool. In contrast to many previous studies that treated communities as being *either* niche or dispersal assembled (e.g., Fargione et al. 2003; Wootton 2005; Dornelas et al. 2006), my general goal is to build a better understanding of *the conditions in which* we would expect these processes to be important in community assembly.

HIGH-DIVERSITY LONGLEAF PINE COMMUNITIES

The longleaf pine (*Pinus palustris*) ecosystem provides a model setting for examining how dispersal and niche-based processes interact to assemble high-diversity plant communities. Three centuries ago, this ecosystem dominated the coastal plain of the southeastern United States, extending from southeastern Virginia to eastern Texas and southward from northern Georgia and Alabama to central Florida (Peet and Allard 1993; Platt 1999), covering a total area of ~38 million ha (Earley 2004). The longleaf pine ecosystem encompasses a broad range of community types (e.g., Peet and Allard 1993 recognized 23 community types), ranging from xeric pine-oak scrub to mesic flatwood-savannas and seasonally wet savannas (Peet and Allard 1993; Sorrie and Weakley 2006). Frequent fire is an important component in these communities, with typical historic fire-return intervals of more than 1 fire per decade (Platt 1999). Four characteristics of these communities make them particularly useful for studying community assembly: (1) extreme levels of small-scale plant diversity in the groundcover plant community, including C_3 grasses, C_4 bunchgrasses, sedges, non-legume forbs, legume forbs, and shrubs; (2) the presence of at least two pervasive niche-based abiotic filters (frequent fire and soil moisture); (3) groundcover communities that are generally dominated by a single functional guild (large-stature bunchgasses) - a potentially competitive, biotic filter for many smaller-stature species; and, (4) local communities that are highly amenable to field experiments relative to other high-diversity communities (e.g., rainforests). Moreover, this ecosystem is among the most threatened in the world: <2% of the original ecosystem remains and most remnant communities are small and fragmented, and those with the highest species richness are actively maintained with prescribed fire (Earley 2004; Keddy et al. 2006). Insight into the ecological mechanisms involved in the assembly of these threatened communities is critical for the restoration, conservation, and management of biodiversity.

Longleaf pine communities support extreme levels of biodiversity. At small scales, they are the most species-rich plant communities in North America and comparable in species richness to other high-diversity grasslands worldwide (Walker and Peet 1983; Peet and Allard 1993; Fridley et al. 2006), reaching a maximum of >50 species/1 m^2 (mean = 35–40 species/1 m^2) and 140 species/1000 m^2 in wet pine savannas (Walker and Peet 1983; Fridley et al. 2006). In comparison, mean species richness in other well-studied temperate grasslands ranges from 16 species/1 m^2 in North-American oak savannas (Cedar Creek Long-Term Ecological Research Site; Tilman 1997), 18 species/1 m^2 in North American tall-grass prairie (Walker and Peet 1983), and 33–39 species/1 m^2 in European chalk and alvar grasslands (Fridley et al. 2006). Levels of endemism are equally striking: Of the 1630 total vascular plant taxa endemic to the entire southeastern coastal plain, 1000 are obligate associates of the longleaf pine ecosystem (Sorrie and Weakley 2006), including 15 endemic genera (Sorrie and Weakley 2001). The mechanisms that contributed to the origin of this biodiversity remain largely unstudied, but are hypothesized to include high variation in soil characteristics (pH and texture) and moisture across the region, relatively infertile soils that limit growth of productive and potentially competitive species, a frequent fire regime, the presence of large refugia for plants during Pleistocene glacial cycles, and dispersal from several surrounding regions (continental tropics, Appalachians, midwestern prairies, and the dry Southwest) during the last 50 million years (Walker and Peet 1983; Sorrie and Weakley 2006).

Hypotheses for the maintenance of biodiversity in longleaf pine communities suggest that three pervasive niche-based ecological filters influence species diversity and coexistence: fire, competition from large-stature plant species, and soil moisture (Walker and Peet 1983; Platt 1999; Kirkman et al. 2001; Brewer 2003; Brewer 2006; Keddy et al. 2006; Platt et al. 2006; Thaxton and Platt 2006; Beckage et al. 2009). At the landscape scale, variation in fire frequency

influences plant-species diversity: in general, more frequent fires promote higher local diversity, presumably by increasing space (e.g., removing litter), availability of other resources (light and nutrients), and by removing woody competitors (Walker and Peet 1983; Brockway and Lewis 1997; Glitzenstein et al. 2003). At local scales, high-intensity fires reduce abundances of large-stature shrubs (Thaxton and Platt 2006) and bunchgrasses (P.R. Gagnon et al., *unpublished data*) and have been hypothesized to help maintain diversity by reducing interspecific competition (Keddy et al. 2006; Platt et al. 2006; Thaxton and Platt 2006; Roth et al. 2008). Finally, observational studies suggest a particularly strong effect of soil moisture on both α diversity (generally higher species richness in mesic and wet sites relative to xeric sites) and β diversity (large changes in species composition across soil-moisture gradients) (Walker and Peet 1983; Peet and Allard 1993; Kirkman et al. 2001). Collectively, these studies suggest several important mechanisms involved in niche-based community assembly.

In contrast, the role of dispersal in shaping community structure has received little attention, especially with regard to how dispersal and niche-based processes potentially interact to influence community assembly. However, two lines of evidence suggest that dispersal can limit species diversity in longleaf pine communities. First, species with low dispersal potential (e.g., gravity- and ant-dispersed species) are often absent from communities that have undergone recent restoration, even when source populations are present in intact communities nearby (Kirkman et al. 2004). Second, large communities connected by experimental corridors have higher species richness than isolated communities (Damschen et al. 2006). These studies suggest that community diversity is limited by dispersal, but it is unknown how the effects of dispersal are influenced by niche-based ecological filters in space and time.

OVERVIEW OF CHAPTERS

In this dissertation, I examine how three niche-based ecological filters—competition, disturbance (local fire intensity), and resource availability (soil moisture)—interact with dispersal to assemble high-diversity longleaf pine savannas. In Chapters 2 and 3, I test the overarching hypothesis that niche-based filters influence the effect of dispersal on local species diversity and composition using two factorial field experiments conducted in a high-diversity mesic pine savanna in southeastern Louisiana. In Chapter 2, I manipulated seed dispersal and two abiotic filters (local fire intensity and soil moisture) to test three hypotheses: high rates of dispersal enhance local diversity; abiotic filters influence the positive effects of dispersal on local diversity; and abiotic filters increase similarity in community composition. In Chapter 3, I manipulated seed dispersal and competition from two common, large-stature guilds (bunchgrasses and shrubs) to test two additional hypotheses: competition from dominant guilds reduces local diversity; and the positive effects of dispersal are dampened in the presence of dominant guilds owing to biotic recruitment limitation. In Chapter 4, I conducted a meta-analysis that synthesizes results from 63 published experiments that examine how dispersal interacts with abiotic and biotic ecological filters to structure local plant species richness across a wide range of plant communities. This analysis allowed me to explore the generality of the hypotheses and results from my field experiments, as well as to build on my general conceptual framework by testing the hypothesis that the effects of dispersal on local species richness are positively related to species diversity and functional diversity in the species pool, especially in disturbed communities in which some ecological filters are relatively weak. Finally, in Chapter 5, I summarize my results, propose a working conceptual model for community assembly in high-diversity pine savannas, discuss broader implications for community assembly and the maintenance of species diversity, and suggest some future research directions.

CHAPTER 2. DISPERSAL AND NICHE-BASED ENVIRONMENTAL FILTERS INTERACT TO ASSEMBLE HIGH-DIVERSITY PLANT COMMUNITIES

INTRODUCTION

Community ecology is currently in a period of rapid synthesis, with an increased emphasis on integrating local processes (e.g., habitat selection, species interactions) with regional processes (e.g., metacommunity dynamics) to understand patterns and dynamics of biodiversity (Leibold et al. 2004; Ricklefs 2004; Vellend in press). Fundamental to this synthesis are pluralistic theories of biodiversity that incorporate elements from two general but contrasting conceptual models. The niche-assembly model views local communities as deterministic, limited-membership assemblages in which local environmental conditions and biotic interactions influence the assembly, diversity, and composition of communities (Chase and Leibold 2003). In contrast, the dispersal-assembly model views local communities as open-membership assemblages in which chance dispersal, immigration history, and demographic stochasticity primarily influence community assembly (Bell 2001; Hubbell 2001; McGill et al. 2006). Although there is an emerging consensus that both deterministic and stochastic processes influence biodiversity and species coexistence (Chase 2003; Tilman 2004; Gravel et al. 2006; Adler et al. 2007), most empirical studies have focused on testing predictions at the extreme ends of this theoretical continuum (e.g., McGill et al. 2006). Consequently, there is a major gap in our understanding of how niche- and dispersal-assembly processes interact in space and time to structure natural communities, a critical gap to bridge in light of current threats to biodiversity owing to global environmental change (Clark 2009).

Here, we examine how niche-based processes associated with environmental heterogeneity interact with dispersal (i.e., immigration) to assemble high-diversity plant

communities. Dispersal assembly is hypothesized to play an important role in high-diversity communities with large potential species pools and where most species are rare and few species are common. An important consequence of rarity in species-rich communities is that populations of many species are recruitment limited owing to reduced fecundity and/or dispersal (Hubbell et al. 1999). Under these conditions, competitive exclusion can be delayed (Hurtt and Pacala 1995), allowing species that arrive to local communities from the potential species pool to persist in those communities, thereby maintaining diversity. Thus, immigration is generally predicted to increase local diversity in high-diversity communities (Hubbell 2001). In addition, dispersal-assembled communities with similar environmental conditions are predicted to have dissimilar species composition, owing to effects of ecological drift and/or stochastic immigration history (Chase 2007), especially in communities assembled from a large species pool (Chase 2003).

Membership in local communities may also depend on the ability of species to tolerate niche-based environmental "filters" imposed by local abiotic or biotic conditions (Keddy 1992; Diaz et al. 1998; Myers and Harms 2009b). Here, dispersal may have little to no influence on local diversity if environmental conditions prevent species from establishing in local communities, e.g., as in species-sorting metacommunity models (Leibold et al. 2004). Alternatively, high rates of dispersal may decrease local diversity if they increase the probability that dominant competitors or predators are introduced into local communities (Mouquet and Loreau 2003). The relationship between dispersal and local diversity will also be influenced by the strength of niche-based filters in space and time: in the presence of an exceptionally strong filter, local diversity may be largely decoupled from dispersal. Finally, in contrast to dispersal-assembled communities, niche assembly is predicted to increase similarity in species composition among communities with similar environmental conditions, especially when those conditions include strong environmental filters (Chase 2003, 2007).

We investigated how dispersal and niche-based environmental filters interact to assemble high-diversity, fire-frequented longleaf pine (*Pinus palustris*) savannas. The longleaf pine ecosystem provides an ideal setting for exploring mechanisms of community assembly in species-rich plant communities, in several important ways. First, at small spatial scales, longleaf pine groundcover communities harbor the highest levels of plant species richness in North America and comparable levels of species richness to other high-diversity grasslands worldwide (up to 40+ species/m^2; 140 species/1000 m^2; Walker and Peet 1983; Peet and Allard 1993). Second, frequent fire is a key component of this ecosystem (Earley 2004). Spatial variation in local fire intensity influences abundances of dominant groundcover species (bunchgrasses and shrubs; Thaxton and Platt 2006; P.R. Gagnon et al., *unpublished data*) and may function as an important niche-based environmental filter influencing local community assembly and species coexistence (e.g., Walker and Peet 1983; Brewer 2006; Platt et al. 2006; Myers and Harms 2009a). Third, observational studies indicate that soil moisture plays an important role in shaping patterns of species richness and composition at multiple scales (Walker and Peet 1983; Peet and Allard 1993; Kirkman et al. 2001), suggesting a second important niche-based filter, especially for seed and seedling recruitment. Finally, this ecosystem has experienced some of the highest levels of habitat destruction worldwide (<2% of the original ecosystem remains), underscoring the need to understand ecological processes that can aid in the conservation or restoration of threatened biodiversity (Earley 2004).

We experimentally tested three mechanistic hypotheses concerning community assembly and the maintenance of local biodiversity in longleaf pine savannas: (1) high rates of dispersal increase local diversity; (2) the positive effects of dispersal on local diversity are influenced by two types of niche-based environmental filters (fire disturbance intensity and soil moisture); and (3) niche-based filters increase similarity in community composition.

METHODS

We conducted our study in an upland, mesic, >100-ha longleaf pine savanna at Camp Whispering Pines, Tangipahoa Parish, Louisiana, USA (30°41′ N, 90°29′ W; mean annual temperature = 19°C, mean annual rainfall 1626 mm, 25–50 m above mean sea level; see Platt et al. 2006). The site has a large potential species pool (>300 vascular plant species) and high species richness at local scales (22 species/0.5 m^2 [this study]; 30 species/1 m^2 [K.E. Harms et al., *unpublished data*]; 103 species/100 m^2 [Platt et al. 2006]), including a diverse groundcover assemblage of forbs, grasses, and shrubs. The relatively fertile soils consist of well-drained sands mixed with and capped by windblown loess (Platt et al. 2006). The site has been restored and maintained with biennial growing-season prescribed fires (April-May; Figure 2.1a) since 1994. Our two-year study was conducted from May 2007 to April 2009 in an area burned in May 2007.

Our study consisted of a 2 x 3 x 2 factorial, split-plot experiment with three treatments: fire disturbance intensity (control [natural, low-intensity fire], high), soil moisture (low, control, high), and seed dispersal (control, high). We randomly assigned disturbance and soil-moisture treatments to 60 2x3-m plots located in two sites (blocks) separated by ~400 m (30 plots/block). Plots were oriented with the long axis north-south, positioned at least 7 m apart and at least 2 m from pine trees, located in areas with relatively homogeneous cover of large-stature bunchgrasses, and, to maximize light availability, located in or just south of gaps in the pine overstorey. In each plot, we randomly assigned dispersal treatments to 2 0.5-m^2 subplots. To reduce edge effects, we positioned subplots 0.5 m inside plots and separated them by 1 m. In order to record locations and densities of plants, we divided each subplot into 50 grid cells with aluminum nails marking the corners of each 10 x 10-cm cell (Figure 2.1d). In total, each treatment combination was replicated 10 times.

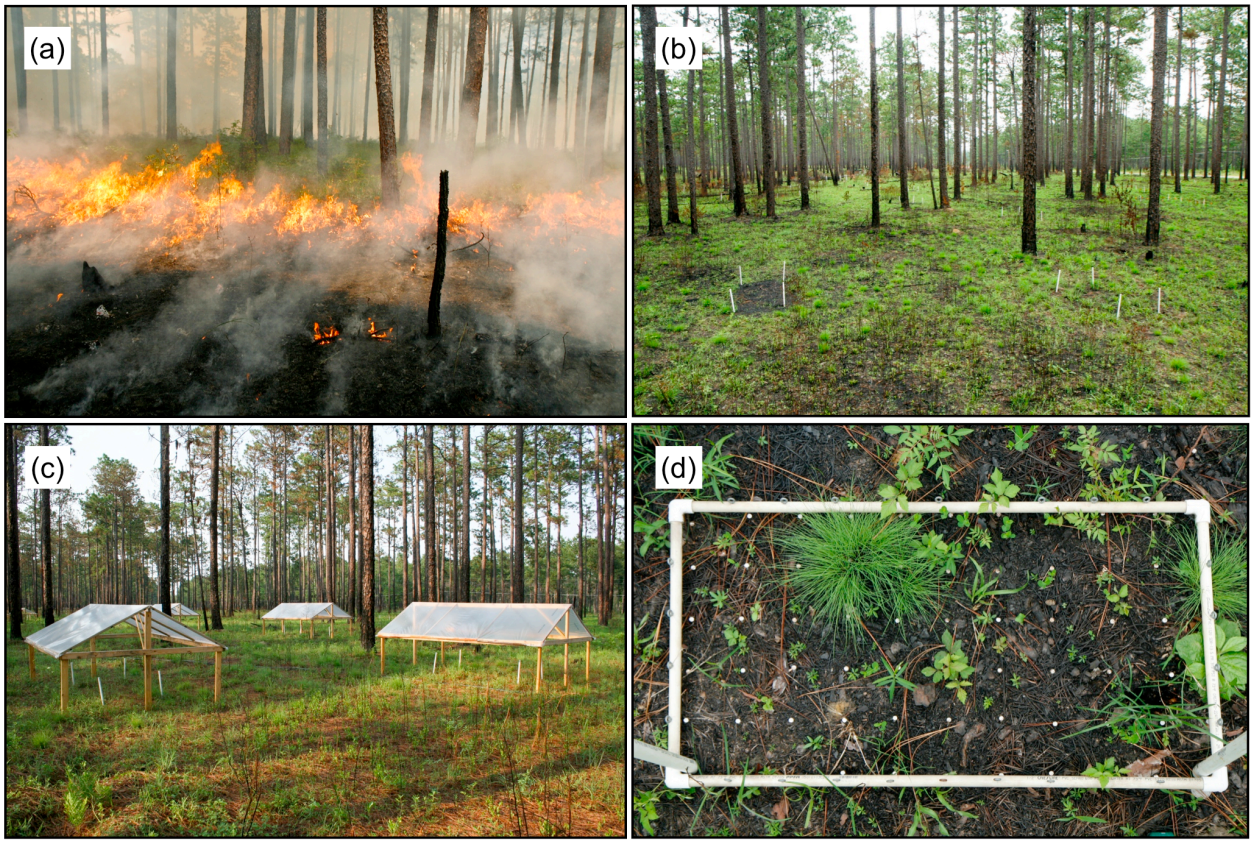

Figure 2.1. Field experiment testing effects of dispersal and environmental filters on community assembly and local biodiversity in a species-rich longleaf pine savanna at Camp Whispering Pines, Louisiana, USA. (a) Prescribed fire. (b) Environmental heterogeneity created by spatial variation in local fire intensity in 6-m^2 plots 1-month post-fire. High-intensity fire (left plot) increased space and decreased biomass relative to low-intensity fire (right plot). (c) Rain shelters used to impose drought conditions on local communities. (d) Local community (0.5-m^2 subplot) 1-month post fire. Photo credits: J.A. Myers.

We manipulated local fire intensity by increasing fine-fuel loads (pine needles) in plots before an early growing-season prescribed fire in May 2007 (Figure 2.1a). On the morning of the fire, we evenly distributed 12 kg of dry pine needles over half of the plots (high-intensity treatment; 2 kg/m^2), mimicking the upper range of observed fuel loads at our study site (Thaxton and Platt 2006). The remaining plots were used as controls and all burned under natural fuel loads.

We manipulated post-fire soil moisture using rain-shelters and irrigation designed to mimic drought and high-rainfall conditions, respectively. In our low soil-moisture treatment, we covered 20 plots (3 x 2 m) with individual rain shelters (3.5-m length x 2.5-m width x 1.5-m height) constructed out of a wooden frame and transparent polyethylene film roof (Tufflite IV 6 mil clear 4-year poly film; Gothic Arch Greenhouses, Mobile, Alabama, USA) 2 weeks after the fire (Figure 2.1c). To minimize temperature and light effects, the frames were left uncovered on both ends and up to ~1 m on both sides. The rain shelters were sufficiently tall to allow unimpeded growth and reproduction of the tallest functional group in the plots (bunchgrasses). In our high soil-moisture treatment, we irrigated 20 plots 3–4 days per week during the growing season (June-Nov. in 2007; June-Sep. in 2008) using an automated sprinkler system connected to the camp's water supply. Plots were watered for 30–60 min. in the early morning and late afternoon. The remaining 20 plots were used as controls and received natural rainfall. Finally, to test for any effects of rain shelters themselves (beyond their effect on soil moisture), we also irrigated 10 additional plots that were also covered with rain shelters. Due to logistical constraints, we could not manipulate fire intensity nor dispersal in these plots, and therefore did not include this treatment in factorial analyses of species richness (described below). Rather, we primarily used this treatment to test whether the effects of rain shelters on biomass, presumably due to drought conditions, were ameliorated when rain shelters were irrigated.

We manipulated dispersal by adding seeds of 31 species of forbs and sedges from the local species pool to one of the two subplots (Appendix A). The other subplot was used as a control and received natural immigration. We added field-collected seeds over a period of 5 months (Jul. – Dec.) as seeds became available, mimicking the timing of natural seed dispersal for most species. The majority of our seed-addition species are gravity- and wind-dispersed forbs, which constitute the most species-rich functional group at the study site (Platt et al. 2006).

We added a total of 4650 seeds/subplot (9300 seeds/m^2), at a median rate of 100 seeds/species/subplot (200 seeds/species/m^2). Approximately half of the added seeds were wind-dispersed forbs (4570 seeds/m^2). Natural total seed densities at our study site average 11666 seeds/m^2, approximately half of which are wind-dispersed forbs (5266 seeds/m^2; Johnson 2006, *unpublished data*). Thus, we estimate that we approximately doubled local seed densities, both at the level of the total pool of seed-addition species and for the most common functional group (wind-dispersed forbs). Seeds of all 30 species tested for germination were viable under growth chamber conditions, with a median germination probability of 65% (range = 12-98%; Appendix A; see Myers and Harms 2009a for germination methods).

We measured species richness, composition, densities of seed-addition species, aboveground biomass, and soil moisture. Species richness, composition, and densities of stems or rosettes (depending on the species) were measured in each of the 120 subplots in three censuses: Sep-Oct. 2007 (5 months post fire); Aug-Sep. 2008 (15 months post fire); and Apr. 2009 (23 months post fire). We sampled biomass in Nov. 2007 (6 months post fire) by clipping all plants at ground level in two stratified sample areas (0.25 m^2 total) located between the two subplots within each plot. Biomass samples were dried at 75°C for 48 hours and then weighed. In June 2008, we measured soil volumetric water content (hereafter "soil moisture") after several rain-free days at two soil depths (7.5 and 20 cm) in each plot using a time domain reflectometer (Field Scout TDR 200; Spectrum Technologies, Inc., Plainfield, Illinois, USA). In each plot, we measured the mean soil moisture based on 4 measurements 5–10 cm outside of the north and south edges of each subplot.

We analyzed total species richness, richness of seed-addition species, total density of seed-addition species, biomass, and soil moisture using linear mixed-effects models (*lme* function in the R *nlme* package; Pinheiro et al. 2009). For species richness and density, we used

repeated-measures models to account for correlation among subplot measurements across the three censuses. Our model for total species richness included the three treatments (fire intensity, soil moisture, dispersal) and census as fixed effects, and blocks, plots (whole-plot factor), and subplots (split-plot factor) as nested random effects. To analyze richness and density of seed-addition species, we only used data from the seed-addition (high dispersal) subplots, which allowed us to explicitly examine the effects of environmental filters on seed-addition species that mostly recruited from seed (most seed-addition species were absent or rare in the control subplots). These models therefore included the two filter treatments and census as fixed effects, and blocks and plots as nested random effects. The same model structure was used for biomass, whereas soil depth was included as an additional fixed effect for soil moisture. When necessary, we $\log_{10}$- or square-root transformed response variables to meet the assumptions of ANOVA. If transformation did not improve homogeneity of variances, we used a heterogeneous variance model (*varIdent* function) and selected the model with the lowest Akaike Information Criterion (AIC).

There were no significant four-way (total species richness) or three-way (all other response variables) interactions, nor were there any significant two-way interactions between fire-intensity and soil-moisture treatments for any response variable. For simplicity, we therefore focus on and present figures showing interactions between the environmental filter and dispersal treatments, and we provide ANOVA results for all two- and three-way interactions in Appendix A.

We analyzed effects of environmental filters on species composition using the R *vegan* package (Oksanen et al. 2009). For these analyses, we focused on composition of seed-addition species in the high-dispersal treatment 23 months post fire, because this allowed us to test for effects of the environmental filters in local communities assembled from a standardized species

pool. First, we created a matrix of community similarity using the abundance-based Bray-Curtis index. Second, we used analysis of similarity (ANOSIM) to test for treatment differences in community similarity separately for the fire-intensity and soil-moisture experiments. Third, we used nonmetric multidimensional scaling (NMDS; *isoMDS* function) to generate a two-dimensional ordination showing differences in community similarity among treatments. We obtained similar results using the incidence-based Jaccard's index, so for simplicity, we only present results based on the Bray-Curtis index.

RESULTS

Local fire intensity influenced aboveground biomass ($P < 0.0001$) but not soil moisture ($P = 0.6839$), whereas soil-moisture treatments influenced both variables ($P = 0.0012$ for biomass; $P < 0.0001$ for soil moisture; Figure 2.2; Appendix A). High-intensity fire decreased mean biomass by ~40% relative to low-intensity (control) fire (Figure 2.2a), resulting in local communities with decreased plant cover and increased space (Figure 2.1b). Low soil moisture decreased mean biomass by 35% relative to control plots, but high soil moisture had no effect on biomass (Figure 2.2b). Moreover, biomass was similar between control and irrigated rain-shelter treatments, indicating that the decrease in biomass under rain shelters reflected low soil moisture. Rain shelters reduced soil moisture by 50–75% across the two soil depths (20 and 7.5 cm, respectively), whereas irrigation increased soil moisture by 75–145% (Figure 2.2d). Soil moisture was lower at shallow depths in rain-shelter plots, but was similar between depths in irrigated plots (soil moisture x soil depth interaction, $P < 0.0001$; Figure 2.2d). In summary, high-intensity fire decreased biomass and increased space, rain shelters decreased soil moisture and biomass, and irrigation increased soil moisture but had no effect on biomass over the short-term.

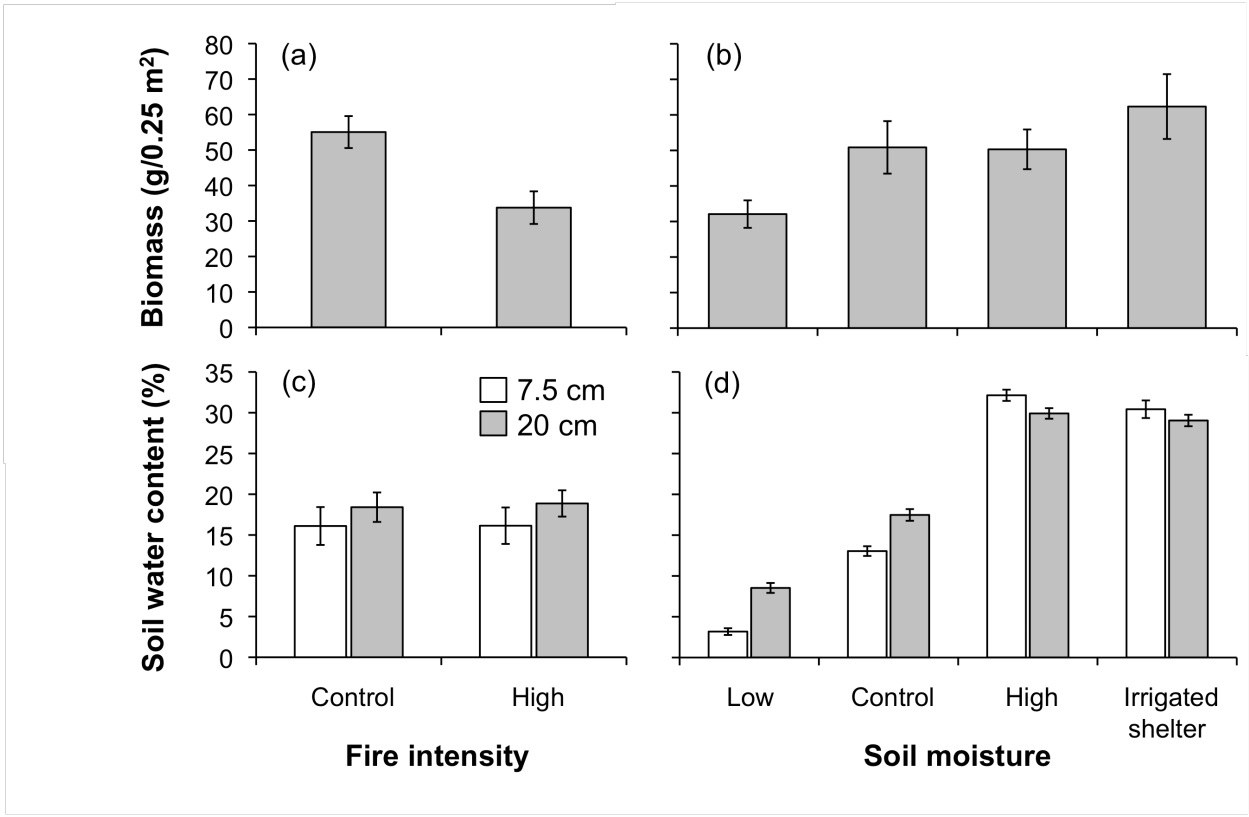

Figure 2.2. Total aboveground dry biomass and soil volumetric water content (soil moisture) in the fire-intensity and soil-moisture treatments. Biomass was measured 6 months post fire and soil moisture was measured during dry summer conditions at two depths (7.5 and 20 cm). Bars = means ± 1 SE; n = 30 (fire intensity), 20 (low [rain shelter], control, and high [irrigation] soil moisture), and 10 plots (irrigated rain shelter).

Dispersal increased total species richness regardless of fire intensity and soil moisture ($P < 0.0001$; Figure 2.3; Appendix A). At the end of the experiment, dispersal increased mean total species richness by 25–50% across environmental-filter treatments (Figure 2.3). Moreover, seed-addition species constituted 40% of the total mean species richness in high-dispersal communities, but only 15% of the species richness in control communities, indicating that the increase in total species richness reflected recruitment of seed-addition species that were initially absent or rare. Of the 31 seed-addition species, 87% (27 species) were present in ≥1 of the high-dispersal communities, and of those species, at least 10 reached reproductive maturity from seed.

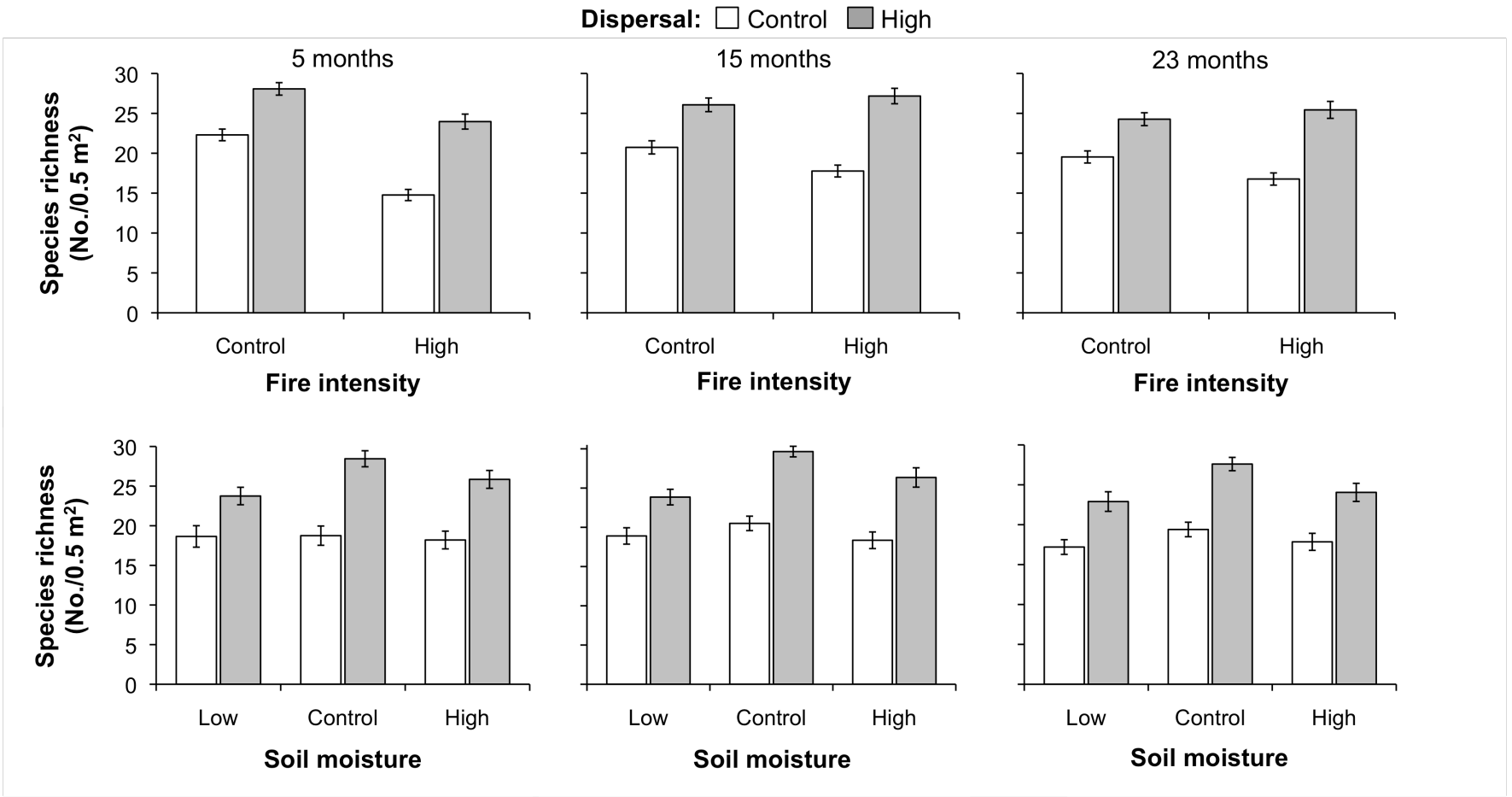

Figure 2.3. Total species richness in the dispersal, fire-intensity, and soil-moisture treatments 5, 15, and 23 months post fire. Bars = means ± 1 SE; n = 30 (fire intensity) and 20 (soil moisture) subplots.

Environmental filters influenced the degree to which dispersal enhanced species richness (Figure 2.3; Appendix A). High-intensity fire decreased total species richness ($P = 0.0006$), primarily in communities with low dispersal (fire intensity x dispersal interaction, $P = 0.0019$). Under low dispersal, high-intensity fire decreased total species richness by 33% in the first growing season, but this effect dissipated with time (fire intensity x time interaction, $P < 0.0001$). Under high dispersal, in contrast, high-intensity fire had little or no influence on total species richness. Moreover, high-intensity fire increased richness of seed-addition species ($P = 0.0121$), especially after the first growing season (fire intensity x time interaction, $P = 0.0060$; Appendix A), as well as the total density of seed-addition species only after the first growing season (fire intensity x time interaction, $P = 0.0214$; Appendix A). Thus, high-intensity fire decreased richness of resident species, yet simultaneously increased recruitment from the species pool.

High and low soil moisture decreased total species richness ($P = 0.0103$), primarily in communities with high dispersal (soil moisture x dispersal interaction, $P = 0.0238$; Figure 2.3; Appendix A). Soil moisture also influenced the richness and total density of seed-addition species ($P = 0.0002$ for richness; $P < 0.0001$ for density). Low soil moisture decreased richness and density of seed-addition species by 30% and 65%, respectively, whereas high soil moisture had no effect on richness of seed-addition species but increased their total density by 25% (Appendix A).

Fire intensity and soil moisture influenced the composition of seed-addition species (Figure 2.4). Communities assembled following high-intensity fire were more similar in species composition than communities assembled following low-intensity fire, but the overall difference was small (ANOSIM, $R = 0.04$, $P = 0.039$; Figure 2.4). High soil moisture significantly increased similarity in species composition relative to low soil-moisture and control treatments

(R = 0.33, $P = 0.001$), but there was no strong difference in composition between low soil-moisture and control treatments (Figure 2.4).

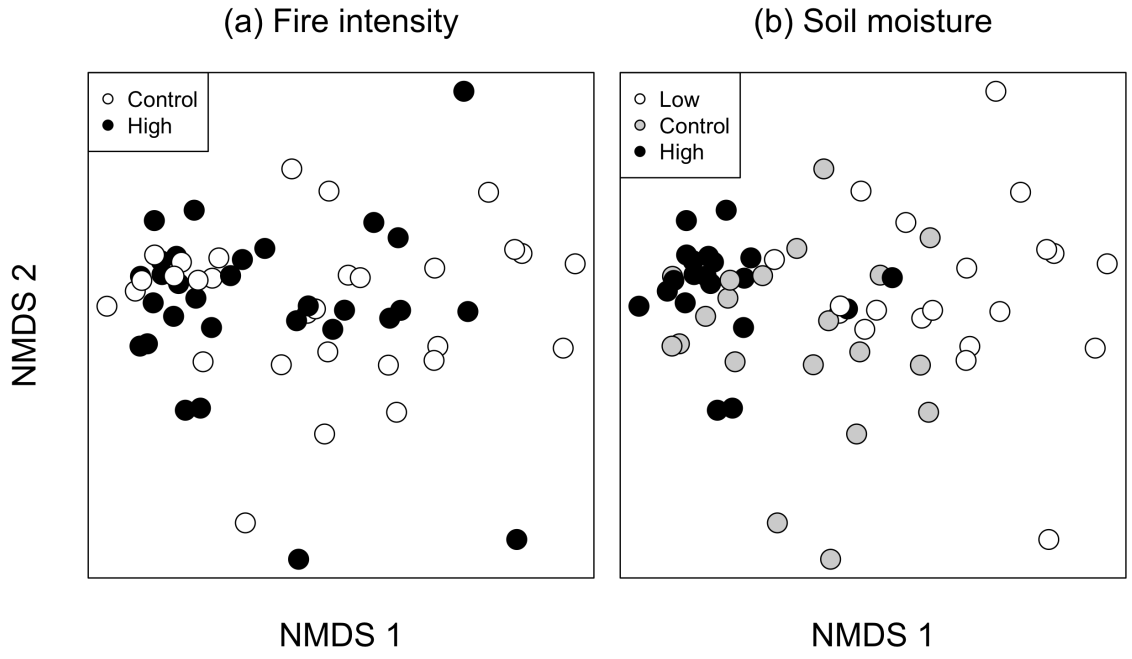

Figure. 2.4. Ordination of seed-addition species composition (Bray-Curtis similarity) in the fire-intensity and soil-moisture treatments 23 months post fire derived from nonmetric multidimensional scaling (NMDS; stress = 0.18). Circles represent replicate subplots (local communities) in the seed-addition (high dispersal) treatment; communities close together in ordination space are more similar in their composition of seed-addition species.

DISCUSSION

Our results support the general hypothesis that dispersal strongly enhances local biodiversity in high-diversity plant communities, but that the importance of dispersal is influenced by niche-based environmental filters. We found that dispersal increased species richness regardless of the intensity of disturbance or soil moisture, but that both types of environmental filters caused recruitment limitation in species added from the species pool. Moreover, we found that communities assembled from a standardized species pool were more similar in species

composition in the presence of strong environmental filters, illustrating conditions under which deterministic, niche-based processes contribute to the assembly of high-diversity communities.

Locally intense fires increased environmental heterogeneity by creating a spatial mosaic of gaps in the landscape (e.g., reduced biomass following high-intensity fire; Figure 2.1, 2.2), caused short-term loss of resident species diversity in the first growing season (Figure 2.3), and enhanced recruitment from the species pool (stronger positive effect of dispersal on species richness following high-intensity relative to low-intensity fire; Figure 2.3). These results suggest that high-intensity fire functions as both an environmental filter that removes some resident species from local communities, as well as a mechanism that reduces the intensity of other niche-based filters such as resource limitation and competition from dominant species, i.e., shrubs and bunchgrasses (Thaxton and Platt 2006; Myers and Harms 2009a). High-intensity fires resulted in local communities with reduced biomass and increased space (i.e., greater potential microsite availability). Over the short term, high-intensity fire can therefore play an important role in the maintenance of species diversity by creating recruitment opportunities for seeds that arrive from the species pool. Over the longer term, variation in fire intensity may help maintain diversity by enhancing individual performance (growth, survival, and/or fecundity) of rare recruits in sites with low densities of competitors (Chesson 2000), as well as by promoting coexistence of species with different post-fire regeneration traits.

Communities assembled following high-intensity fire were more similar in composition of seed-addition species relative to communities with low-intensity fire, but the overall difference among these communities was small. High-intensity fires may contribute to deterministic community assembly by filtering species that lack traits required to survive through intense fire or recruit in post-fire environments, promoting recruitment of gap-dependent species. Although our experiment primarily focused on recruitment of the most species-rich functional

group at our study site (gravity- and wind-dispersed forbs), it is likely that we would have uncovered a stronger, deterministic effect of disturbance if we had expanded our experimental species pool to include greater functional diversity (Questad and Foster 2008; Myers and Harms 2009b).

We expected that low soil moisture would reduce recruitment from the species pool, but that high soil moisture would have the opposite effect, owing to positive effects of soil moisture on recruitment and species richness (e.g., Kirkman et al. 2001; Foster and Dickson 2004). In contrast, we found that species richness was reduced under both low and high soil moisture, likely reflecting seed and seedling mortality under both drought and saturated soil conditions. Moreover, communities assembled under high soil-moisture conditions were more similar in species composition relative to communities assembled under drought and control conditions. This result suggests that high-rainfall conditions function as a niche-based filter that decreases stochasticity in community assembly, a process that, interestingly, parallels effects of drought in aquatic mesocosm communities (Chase 2007). The mechanisms underlying this pattern could reflect niche-based differences in the tolerance of seeds and seedlings to soil moisture (Silvertown et al. 1999) and/or competitive dominance of some seed-addition species under high soil moisture. The higher variability in community composition under low soil moisture, by contrast, may have been more influenced by stochastic loss of individuals and species owing to small population sizes imposed by drought conditions, as well as by higher variation in soil moisture under rain shelters relative to irrigated communities.

Our study contributes to a broader understanding of community assembly and the maintenance of biodiversity in high-diversity plant communities. First, our results underscore the importance of synthetic models in community ecology that integrate effects of dispersal and niche assembly to understand when, and under what conditions, communities are assembled by

stochastic and deterministic processes (e.g., Chase 2003; Gravel et al. 2006; Chase 2007). Although there is growing experimental evidence that seed arrival from local and regional species pools limits local diversity in species-rich plant communities (Zobel et al. 2000; Damschen et al. 2006; Myers and Harms 2009a; Paine and Harms 2009), our results suggest that niche-based recruitment limitation during seed and seedling establishment constrains effects of dispersal on community assembly in space (e.g., variation in disturbance intensity) and time (drought vs. high-rainfall years). Second, frequent fire in longleaf pine communities plays an important role in limiting abundances of common species and promoting recruitment of rare species from the species pool, paralleling effects of grazers in chalk grasslands and natural enemies in tropical forests (Silvertown 2005), suggesting intriguing commonalities in the general mechanisms that maintain extremely diverse plant communities. Finally, our results can help guide restoration and conservation of highly endangered pine savannas under changing rainfall conditions, especially in fragmented and isolated communities where biodiversity restoration requires a combination of prescribed fire and seed introductions from the regional species pool.

CHAPTER 3. LOCAL IMMIGRATION, COMPETITION FROM DOMINANT GUILDS, AND THE ECOLOGICAL ASSEMBLY OF HIGH-DIVERSITY PINE SAVANNAS*

INTRODUCTION

The mechanisms maintaining biodiversity in ecological communities can be envisaged as falling along a dynamic continuum bounded by two general models (Hubbell 2001; Gravel et al. 2006). At one extreme are niche-assembly models that view communities as deterministic, limited-membership assemblages in which interspecific competition for limiting resources and space and other biotic interactions determine species' presence and abundance (Hutchinson 1957; MacArthur and Levins 1967; Tilman 1982; Chesson 2000; Chase and Leibold 2003). On the other extreme are dispersal-assembly models that view communities as stochastic, open-membership assemblages in which immigration history, chance dispersal events, and demographic stochasticity primarily influence community structure (MacArthur and Wilson 1967; Sale 1977; van der Maarel and Sykes 1993; Bell 2000; Hubbell 2001). Synthesis of these concepts into a unified model of biodiversity and species coexistence remains a major goal of ecology (Agrawal et al. 2007), and recent theory incorporating deterministic and stochastic processes has gone a long way in moving this synthesis forward (Chase 2003; Tilman 2004; Gravel et al. 2006). A fundamental gap remains, however, in our empirical understanding of where many natural communities fall along this continuum. Here we explore how one key component of niche assembly (competition from dominant guilds) and dispersal assembly (local immigration) interact to structure local biodiversity in a high-diversity plant community.

*Reprinted from *Ecology* with permission from the Ecological Society of America. Citation: Myers, J. A. and K. E. Harms. 2009. Local immigration, competition from dominant guilds, and the ecological assembly of high-diversity pine savannas. Ecology 90:2745-2754.

In high-diversity communities, most species are rare and coexist with few common species. This high degree of rarity has at least three important implications for community assembly. First, rarity increases the importance of demographic stochasticity in community dynamics (Barot 2004). Local extinctions of rare species owing to demographic stochasticity reduce the importance of deterministic processes in community assembly. Second, populations of many species in high-diversity communities may be recruitment limited (Hubbell et al. 1999), which can slow rates of local extinction owing to competitive exclusion (Hurtt and Pacala 1995). Under these first two conditions, stochastic dispersal and immigration history can exert a strong influence on community structure, especially in high-diversity communities assembled from large local and regional species pools (Eriksson 1993). Third, rarity limits the degree to which species interact. Consequently, pairwise interactions between rare species occur infrequently, further limiting the degree to which deterministic interactions contribute to community assembly (Grubb 1986; Hubbell and Foster 1986). However, this does not necessarily mean that all species interactions in high-diversity communities are diffuse; interactions between rare and common species can be relatively more predictable in space and time. The strength of these interactions is expected to increase when common species are also of large stature, i.e., when size asymmetries among competing species are large (Keddy and Shipley 1989). Here we test the general hypothesis that local biodiversity reflects the interplay of competition from common, large-stature guilds and local immigration by rare, small-stature species.

Theoretical models predict that high rates of immigration from local and regional species pools increase local species diversity (MacArthur and Wilson 1967; Hubbell 2001; Mouquet and Loreau 2003). What remains controversial, however, is the extent to which the immigration-diversity relationship is influenced by local species interactions (Mouquet and Loreau 2003). Recruitment limitation owing to increased competition or predation has been hypothesized to

reduce positive effects of dispersal on diversity (Kneitel and Miller 2003), and this mechanism of community assembly is thought to increase in importance as productivity increases (Grime 1973). We refer to this mechanism as ‘‘biotic recruitment limitation’’ to distinguish it from recruitment limitation owing to seed limitation or establishment limitation due to abiotic conditions (Nathan and Muller-Landau 2000). Experimental studies in plant communities have revealed that positive effects of immigration on diversity are often greater in disturbed relative to undisturbed sites (Zobel et al. 2000; Foster 2001; Gross et al. 2005). Although these studies suggest an important role for competition at the community level in limiting species membership from local and regional species pools, they provide limited insight into how patterns of seed arrival contribute to local biodiversity in the face of competition from dominant species or guilds. This mechanism of biotic recruitment limitation may play a key role in limiting the extent to which dispersal assembly influences local biodiversity.

We examined how competition from dominant guilds and local immigration interact to structure biodiversity in high-diversity longleaf pine (*Pinus palustris*) savanna groundcover assemblages. From a global perspective, longleaf pine savannas constitute one of the most species-rich plant communities at small spatial scales (40 species/1 m^2, 140 species/1000 m^2), often containing two to three times more species in a square meter than other North American grasslands and similar or higher numbers than other high-diversity grasslands in Europe and Africa (Walker and Peet 1983; Cowling et al. 1994; Fridley et al. 2006; Keddy et al. 2006). We experimentally tested three general hypotheses concerning the maintenance of local biodiversity: (1) competition from common, large-stature guilds reduces diversity; (2) immigration of rare, small-stature species enhances diversity; and (3) positive effects of immigration are dampened in the presence of large-stature guilds owing to biotic recruitment limitation. We tested these hypotheses using two factorial experiments in which we manipulated immigration of 38 small-

stature species and competition from two dominant guilds (large-stature bunchgrasses and shrubs).

METHODS

The longleaf pine savanna ecosystem formerly covered >370000 km^2 of the southeastern United States (Earley 2004). Historically, natural lightning-season fires burned these savannas one or more times per decade (Platt 1999). Presently, <2% of the original ecosystem remains, owing to widespread logging, land clearance, and fire suppression (Earley 2004). Most remnant pine savannas exist in a fragmented network of sites, many of which are being restored or maintained with prescribed fires (e.g., Keddy et al. 2006).

We conducted our study at a remnant and restored >100-ha longleaf pine savanna at Camp Whispering Pines, Tangipahoa Parish, Louisiana, USA (30°41′ N, 90°29′ W; mean annual temperature = 19°C, mean annual rainfall 1626 mm, 25–50 m above mean sea level). Camp Whispering Pines has a large species pool (>300 vascular plant species) and a diverse assemblage of groundcover forbs, grasses, and shrubs at small scales (15 species/0.25 m^2, 22 species/0.5 m^2 [J. A. Myers and K. E. Harms, *unpublished data*], 30 species/1 m^2 [K. E. Harms et al., *unpublished data*], and 103 species/100 m^2 [Platt et al. 2006]). The fertile soils consist of well-drained Pleistocene-aged sands mixed with and capped by windblown loess (Platt et al. 2006). The site has been managed with biennial growing-season prescribed fires (April–May) since 1994 and has never been plowed. Our study was conducted from June 2006 to June 2008 in a site burned in May 2005 and 2007. Platt et al. (2006) provide additional details on the study site.

Experimental Design

Our study consisted of two factorial randomized block experiments, one for bunchgrasses and one for shrubs, involving two main treatments: competition and local immigration. Immigration

treatments were identical for the two experiments, whereas competition treatments differed according to the biology of each dominant guild. We used one common species within each guild for the experiments: the bunchgrass *Schizachyrium tenerum* (Poaceae) and the shrub *Ilex glabra* (Aquifoliaceae). These species are among the most abundant of their respective dominant guilds, i.e., bunchgrasses and shrubs, at the site (Thaxton and Platt 2006; P. R. Gagnon et al., *unpublished data*). *Schizachyrium* is a perennial, C_4 bunchgrass that attains heights up to 1 m, with spreading foliage often lying flat on the ground. Ilex is an evergreen, rhizomatous shrub that reaches heights of 1.5–2 m. At the landscape scale, Ilex tends to be patchily distributed and occurs as large clonal thickets in the otherwise bunchgrass-dominated groundcover layer and is considered an invasive native species in wetter pine savannas (Hinman et al. 2008). When present at local scales, reproductive adults of both species can account for >90% of total aboveground community biomass (mean dominance/0.25 m^2: 92% and 98% for *Schizachyrium* and *Ilex*, respectively; n = 10 plots sampled in fall 2006). We will henceforth refer to the two species generally as bunchgrasses and shrubs.

The two experiments consisted of a 3 x 2 design (competition x immigration) for bunchgrasses and a 2 x 2 design for shrubs. In each experiment, we established 10 replicate blocks with a minimum distance of 5 m between neighboring blocks. We chose block locations on the basis of having sufficient abundances of bunchgrasses or shrubs; for shrubs, a block usually consisted of a single large clone. We randomly applied treatments to 0.5 x 0.5 m plots within blocks (n = 4 or 6 plots/block for shrubs and bunchgrasses, respectively). Plots were oriented in the same cardinal direction (north–south), separated by at least 0.5 m, and located at least 2 m from pine trees. We selected plots on the basis of having similar cover of bunchgrasses or shrubs; *Ilex* shrubs were absent from all bunchgrass plots and *Schizachyrium* bunchgrasses were absent from all shrub plots. We reduced edge effects in two ways: (1) by positioning shrub

plots at least 0.5 m inside each clone; and (2) applying competition treatments inside each plot and in a 0.25 m wide buffer strip around plots in both experiments. In order to facilitate data collection at multiple scales, we divided each plot into 25 grid cells with aluminum nails marking the corners of each 10 x 10 cm cell.

Competition Treatments

Our competition treatment had three levels: (1) control; (2) cover reduction (bunchgrass experiment only); and (3) removal. To reduce effective bunchgrass cover, without disturbing soil or removing ramets, we gathered bunchgrass foliage together into uncut vertical sheaves and bound them using plastic ties. These ties were removed prior to a prescribed fire at the study site in May 2007; bunchgrasses were retied 4.5 weeks later after attaining sufficient size. To remove bunchgrasses, we carefully applied herbicide (Roundup, Scotts, Marysville, Ohio, USA) to bunchgrass foliage with a paintbrush, removing dead litter <1 week later. The removal treatment mimicked complete bunchgrass mortality (e.g., from a locally intense fire), whereas the cover reduction treatment allowed us to explicitly examine effects of belowground competition when aboveground competition was reduced. We removed shrubs by repeatedly clipping individual stems at ground level. To avoid killing entire clones, we did not apply herbicide to shrubs.

Immigration Treatment

Our immigration treatment had two levels: control and increased seed rain. To increase immigration into plots, we added seeds of 38 small-stature, mostly rare forbs and sedges spanning 31 genera and 12 families (Appendix B); we will henceforth refer to these as ‘‘focal species.’’ Most of the species are gravity- or wind-dispersed nonlegume forbs, representing the most species-rich functional group in the local species pool at the study site (Platt et al. 2006). All but one of the 38 species (*Plantago virginica*) are perennial. We hand-collected seeds in the field from multiple, spatially separated plants to ensure a variety of genotypes. Because our focus

was on patterns of community diversity and not effects of treatments on individual species per se, we did not add the same number or mass of seeds for each species. Accordingly, interspecific differences in seed numbers in part reflected seed availability and thus species relative abundance in the local species pool. In contrast to most previous seed addition experiments (e.g., Tilman 1997; Zobel et al. 2000; Foster 2001; Gross et al. 2005), we added species to plots as seeds became available, rather than as a single seed dispersal event. This method better matches temporal patterns of natural seed rain. Our seed additions spanned two time periods: August-September 2006 and July-November 2007, following a prescribed fire in May 2007.

The goal of our seed addition experiment was to increase immigration into plots at levels that fall within natural levels of potential local seed rain. In a two-year study of local seed densities in 1-m^2 plots across four longleaf pine savanna sites in southeastern Louisiana, E. I. Johnson (2006 and *unpublished data*) recorded mean total seed densities ranging from 600 to 11666 seeds/m^2 across sites, with the highest mean densities recorded at our study site (Camp Whispering Pines). Wind-dispersed forbs in the family Asteraceae accounted for approximately half of the total density (mean = 5266 seeds/m^2; E. I. Johnson, *unpublished data*). In 2006, we added 15 total species at a median rate of 30 seeds/species/plot (120 seeds/species/m^2, 4840 total seeds/m^2; Appendix B). In 2007, we added 30 species (23 of which were not added in 2006) at a median rate of 50 seeds/species/plot (200 seeds/species/m^2, 11980 total seeds/m^2). The higher numbers of seeds added in 2007 reflected higher fecundity after the 2007 fire. The most common functional group in our pool of seed addition species was wind-dispersed Asteraceae, accounting for 38% of the total seed density and 36% of the total species richness. Overall, these levels of immigration fall within the range of natural levels of potential local seed rain at the site, both at the level of the entire pool of seed addition species and for the most-common functional group

within the pool. In addition, our seed addition treatment generated plant densities that fall within the natural range of focal species' densities observed at the study site (Appendix B).

In 2007, we tested seed viability (Appendix B) in a climate-controlled growth chamber. Light (16-h day length), temperature (32°C day, 22°C night), and relative humidity (90% day, 50% night) were set to approximate growing-season conditions. For each species, we placed 50 seeds on moist filter paper in a petri dish wrapped in parafilm, remoistened and rotated dishes regularly, and recorded germination for six months. After six months, we cold-stratified dishes at 58°C for one month and recorded germination for another two months. Seeds of all 30 species added in 2007 were viable, with a median germination rate of 56% (range = 4–98%; Appendix B); seed viability was not tested in 2006. To aid with field identification, we raised seedlings of all focal species from seeds in small pots and photographed them at various ontogenetic stages.

Data Collection and Analysis

We measured total species richness, richness of focal species (species added in the immigration treatment), and abundances of focal species in September 2007 and June 2008. The majority of focal species were not present in plots before the start of the experiment. Thus, we used focal species richness and abundances to assess the extent to which recruitment limitation influences community assembly during the juvenile stage and beyond. We measured total species richness at two spatial scales: plot (0.25 m^2) and neighborhood (0.01 m^2). We measured focal species abundance using stem or rosette densities (depending on the morphology of the species).

We examined treatment effects on total and focal species richness using mixed-model ANOVA. Competition and immigration treatments were modeled as fixed effects and blocks as random effects. For the neighborhood-scale analysis, we used the mean species richness calculated from all 25 10 x 10 cm grid cells in each plot (individual grid cells were not modeled as replicate subplots), yielding identical sample sizes for the neighborhood- and plot-scale

analyses (n = 10 per treatment combination). When necessary, response variables were $\log_{10}$- or square-root transformed to meet assumptions of homogeneous variances and normally distributed errors. When transformation did not improve homogeneity of variance, we reran the analysis using a heterogeneous variance model (*varIdent* function in the R *nlme* library) and selected the model with the lowest Akaike Information Criterion (AIC).

We also tested for treatment effects on overall patterns of focal species diversity and evenness by comparing 95% confidence intervals of slopes from rank–abundance curves using linear regression (Magurran 2004). For each treatment, we calculated the mean relative abundance of all focal species present in $\geq$1 plot. For the immigration treatments, we used the pooled data from the competition treatments (n = 30 or 20 for the bunchgrass and shrub experiments, respectively). For the competition treatment, we only used data from the seed addition plots (n = 10 in both experiments). This allowed us to explicitly examine effects of competition on focal species that recruited mostly from seed, as seed control plots contained relatively few focal species. For one analysis (shrub competition), we $\log_{10}$-transformed species ranks to normalize residuals, although we obtained the same qualitative results using untransformed data. Residuals were normally distributed in all other analyses (Shapiro-Wilk tests, $P > 0.07$). We performed all statistical analyses in R (R-Development-Core-Team 2008).

RESULTS

Immigration increased total species richness in both bunchgrass and shrub-dominated plots, but the effects of competition varied between the two dominant guilds (Figures 3.1 and 3.2; Appendix B). In bunchgrass-dominated plots, immigration increased species richness in both years at both the plot (Figure 3.1A, B) and neighborhood (Figure 3.1C,D) scales. Contrary to our predictions, however, there were no significant effects of reduced cover or removal of bunchgrasses on species richness at the plot scale (Figure 3.1B), despite a positive effect of

bunchgrass removal at the neighborhood scale in the second year (mean increase of 0.7 species/0.01 m^2; Figure 3.1D). There were also no significant interactive effects of immigration and bunchgrass competition on total species richness. In the second year, immigration increased total richness by 40–60% at the neighborhood and plot scales, respectively (Figure 3.1B, D). Competition had a smaller overall effect on total richness (9–28% in the removal treatment in the second year).

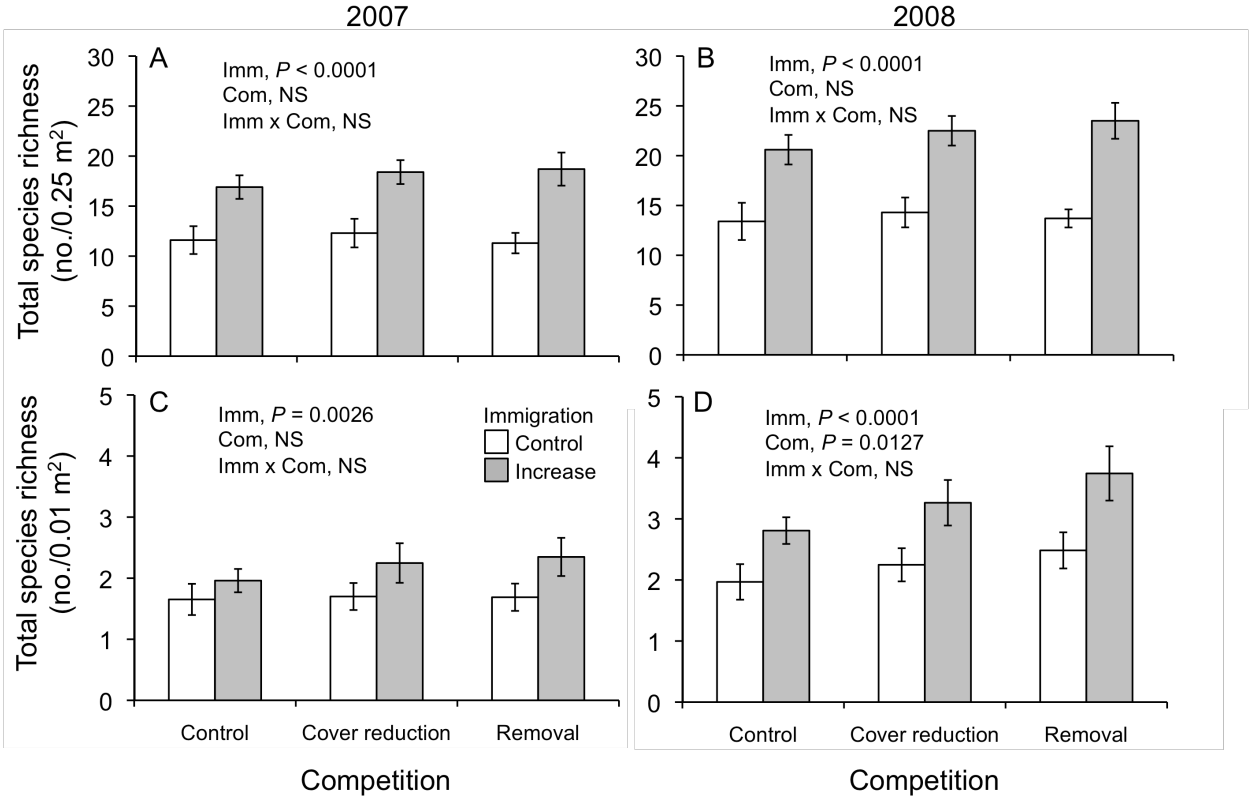

Figure 3.1. Total species richness in the immigration and competition treatments in bunchgrass-dominated plots over two years in a high-diversity longleaf pine savanna at the (A, B) plot scale (0.25 m^2) and (C, D) neighborhood scale (0.01 m^2). Bars = means ± 1 SE; n = 10 plots/treatment. P-values from two-way ANOVA testing main effects of immigration (Imm) and competition (Com) treatments and their interaction (Imm x Com) are listed in each panel (NS = $P > 0.05$).

Total species richness of shrub-dominated plots, in contrast, increased in response to both immigration and competitor removals at both spatial scales (Figure 3.2; Appendix B). The only exception to this general pattern was at the neighborhood scale in the first year, in which

immigration, but not competition, influenced species richness (Figure 3.2C). As with the bunchgrass-dominated plots, there were no significant interactions between the two treatments on total species richness. In the second year, overall effects of immigration on species richness ranged from 70% to 87% at the neighborhood and plot scales, respectively. Overall positive effects of competitor removals ranged from 45% to 100% at the two spatial scales. In summary, local immigration enhanced total species richness in both bunchgrass and shrub-dominated sites, but competition generally reduced richness only in sites dominated by large-stature shrubs.

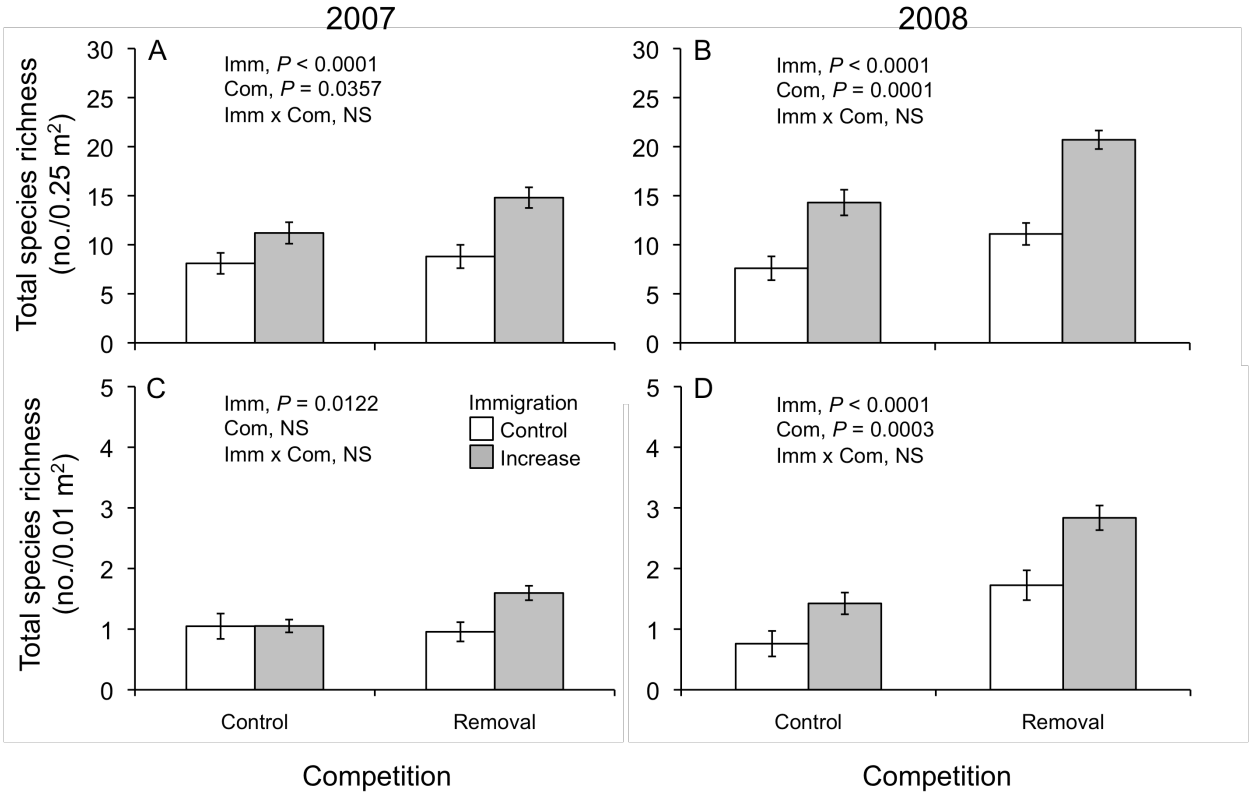

Figure 3.2. Total species richness in the immigration and competition treatments in shrub-dominated plots over two years at the (A, B) plot scale (0.25 m^2) and (C, D) neighborhood scale (0.01 m^2). Bars = means ± 1 SE; n = 10 plots/treatment. P-values from two-way ANOVA testing main effects of immigration (Imm) and competition (Com) treatments and their interaction (Imm x Com) are listed in each panel. Data in panel (C) were $\log_{10}$ transformed before analysis (untransformed data shown).

Focal species richness (species added in the immigration treatment) paralleled patterns of total species richness: immigration increased focal richness in plots dominated by both large-

stature guilds, but competition reduced focal richness only in shrub-dominated plots (Figure 3.3; Appendix B). Immigration increased focal richness in both years, whereas competition from shrubs decreased richness only in the second year. In bunchgrass-dominated plots, there was a marginally significant interaction between treatments on focal species richness, potentially reflecting a stronger positive effect of immigration in the competition reduction and removal treatments relative to the control (Figure 3.3B). Overall, immigration increased focal richness by a factor of 2.7 (bunchgrass) and 3.4 (shrub), whereas removal of shrub competitors increased richness by a factor of 0.6.

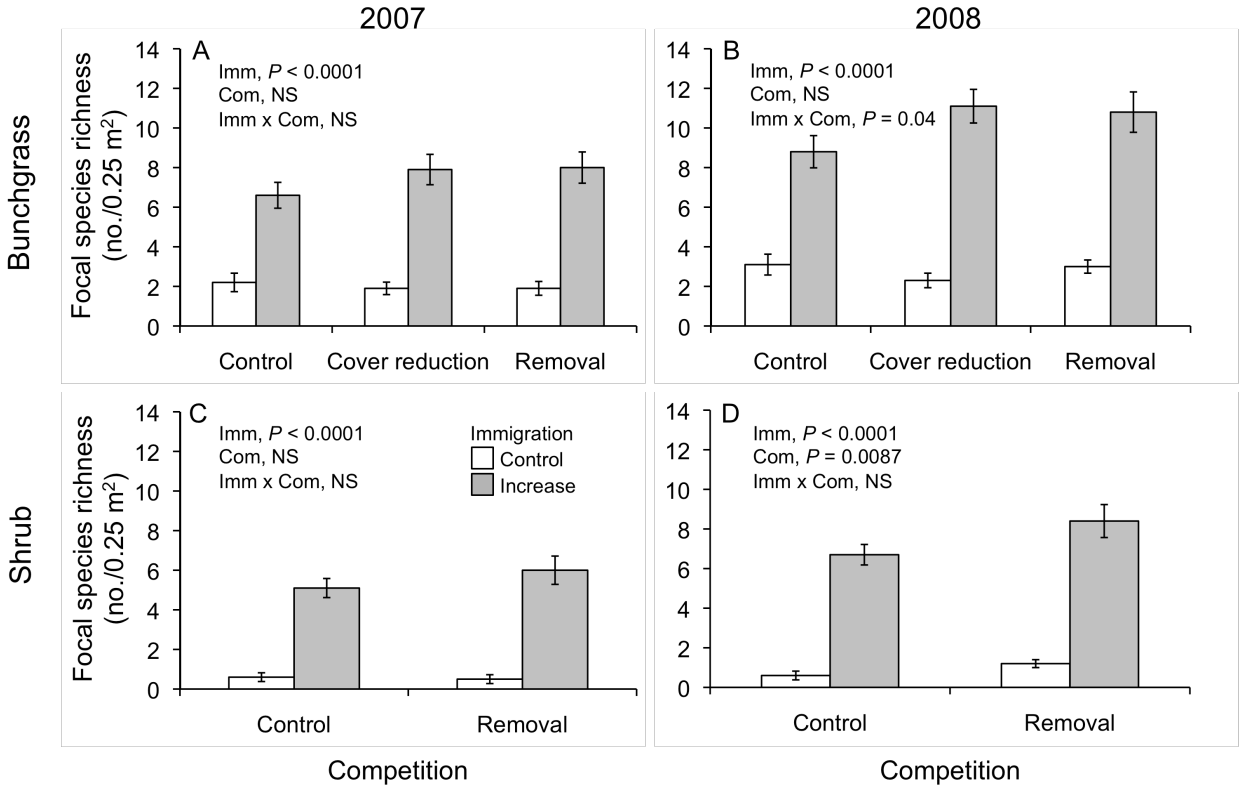

Figure 3.3. Richness of seed-addition (focal) species in the immigration and competition treatments in (A, B) bunchgrass-dominated and (C, D) shrub-dominated plots over two years. Bars = means ± 1 SE; n = 10 plots/treatment. P-values from two-way ANOVA testing main effects of immigration (Imm) and competition (Com) treatments and their interaction (Imm x Com) are listed in each panel (NS = $P > 0.05$). Data in (B) were square-root transformed and data in (D) were $\log_{10}$ transformed before analysis (untransformed data are shown).

Immigration significantly influenced rank–abundance distributions of focal species, whereas competition had no clear effect (Figure 3.4). Immigration increased diversity and evenness of focal species in plots dominated by both guilds, indicated by the steeper slopes of the rank– abundance curves in the seed control relative to seed addition plots (Figure 3.4A, C). In contrast, slopes were similar among competition treatments for both dominant guilds (Figure 3.4B, D).

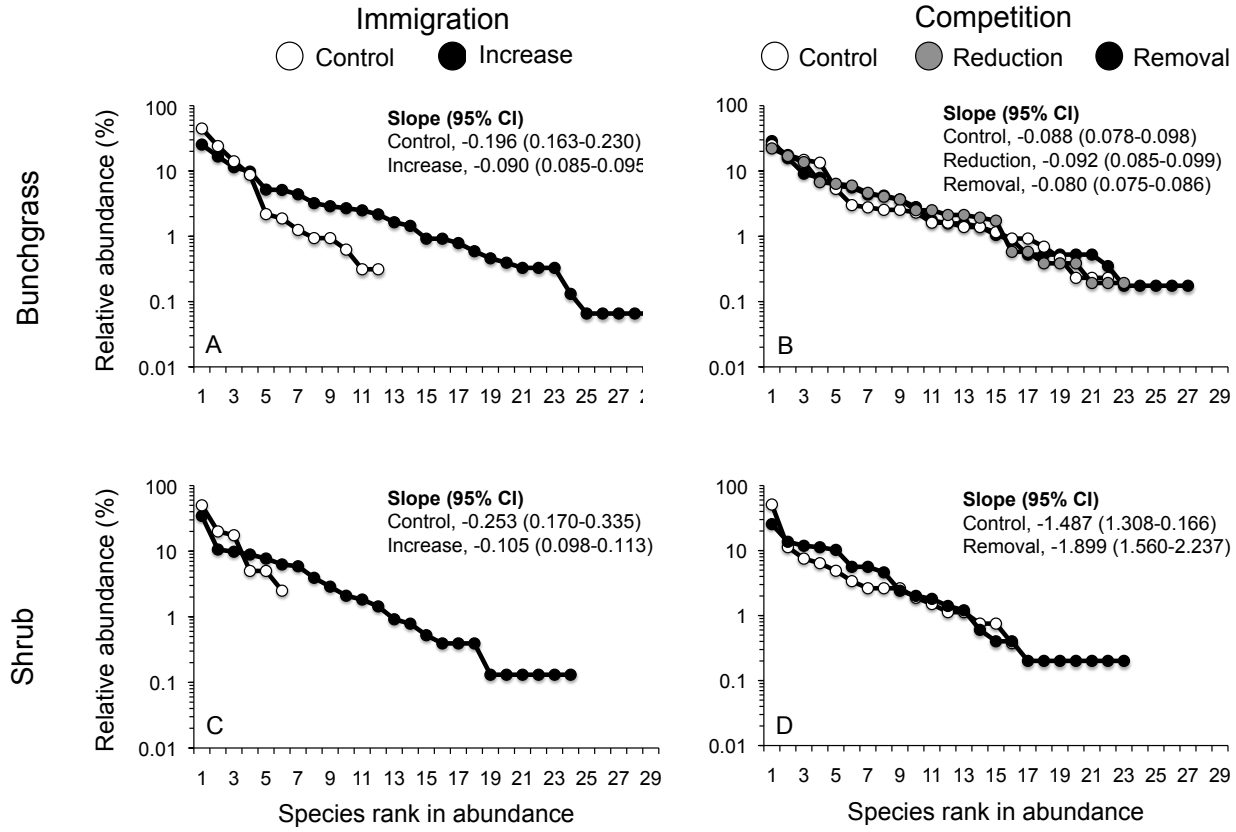

Figure 3.4. Rank-abundance curves for seed-addition (focal) species in the immigration and competition treatments in (A, B) bunchgrass-dominated and (C, D) shrub-dominated plots in 2008. *Plantago virginica*, an annual species that established and reproduced in 2007, is included in the figure. Estimated slopes (and 95% confidence intervals) from linear regression are shown for each treatment. Slopes and confidence intervals in panel (D) were calculated using $\log_{10}$-transformed species ranks (to normalize residuals). Each point represents the abundance of each established focal species averaged across all plots in a treatment (Appendix C); (A) $n = 30$, (C) $n = 20$ (C), and (B, D) $n = 10$ plots/treatment.

Of the 38 focal species, 29 (76%) and 24 (63%) were present in at least one of the seed addition plots in the bunchgrass and shrub experiments, respectively (Figure 3.4A, C; Appendix B). In contrast, only 15–31% were present in seed control plots (Figure 3.4A, C; Appendix B). Collectively, these results indicate a strong role for local immigration in maintaining high diversity, a limited effect of competition on diversity in bunchgrass-dominated plots, and that many species can recruit in shrub-dominated plots despite negative effects of shrub competition on overall patterns of species richness.

DISCUSSION

Our results demonstrate key roles for both local immigration and competition from dominant guilds in the assembly of an exceptionally high-diversity plant community. In support of our general hypothesis, we found that immigration enhanced local species richness and diversity in sites dominated by two common, large-stature guilds, at both neighborhood and plot scales. In contrast, we generally found less significant effects of competition from dominant guilds on local biodiversity, owing to: (1) limited evidence that competition from bunchgrasses, one of the most common large-stature functional guilds in this community, reduces species richness; and (2) similarities in species rank–abundance distributions among competition treatments. These patterns suggest a key role for dispersal assembly in structuring local biodiversity in this high-diversity plant community, but that the importance of this mechanism depends on the strength of local niche assembly involving competition from some, but not all, dominant guilds.

Local Immigration and Competition from Dominant Guilds

We hypothesized that positive immigration–diversity relationships would be dampened in sites dominated by common, large-stature species (Kneitel and Miller 2003; Mouquet and Loreau 2003). However, we generally found positive effects of local immigration regardless of levels of competition from bunchgrasses and shrubs (i.e., no strong interactive effects of local

immigration and competition on species richness), indicating that rare species can recruit in the face of potential competition from dominant guilds. Under favorable abiotic conditions in the field, at least eight of these focal species can recruit from seed and become reproductive adults by the end of their first two growing seasons (J. A. Myers and K. E. Harms, *unpublished data*).

The positive immigration–diversity patterns observed in our study may be influenced by several mechanisms. First, these effects can be transient or reduced as competition intensifies over longer time scales, e.g., when time between disturbance increases or as individuals and populations increase in size. Under these conditions, the importance of deterministic species interactions may increase through time, even in communities initially assembled by stochastic dispersal (e.g., ‘‘noninteractive’’ vs. ‘‘interactive’’ phases of community assembly; Emerson and Gillespie 2008). Second, positive immigration–diversity patterns may persist when frequent disturbances reduce or remove dominant competitors and litter (Grime 1973) or via local mass effects (Shmida and Ellner 1984; Leibold et al. 2004). In longleaf pine savannas, frequent, locally intense fires increase mortality of shrubs (Thaxton and Platt 2006) and bunchgrasses (P. R. Gagnon et al., *unpublished data*) and therefore may contribute to longer-term coexistence of dominant and rare guilds. Third, recruitment limitation owing to limited fecundity and dispersal prevents rare species from reaching many sites that they would otherwise occupy (Hubbell et al. 1999; Nathan and Muller-Landau 2000). Although dispersal limitation is often viewed as a key mechanism contributing to stochastic community assembly (Hubbell 2001), dispersal limitation can differ among species in important ways that influence niche assembly (Clark 2009) and generate similar results in models built from niche and neutral mechanisms (Adler et al. 2007). Interestingly, the effects of dispersal on biodiversity may therefore include both deterministic (dispersal traits linked to species’ niches) and stochastic (e.g., priority effects and stochastic seed arrivals) components.

Given the importance of size asymmetries in determining the position of species along competitive hierarchies (Keddy and Shipley 1989), we expected smaller competitive effects of bunchgrasses relative to shrubs. Nevertheless, we predicted competition from bunchgrasses to leave a strong signature on patterns of species diversity. However, we found limited effects of bunchgrass competition on diversity, a pattern not consistent with the hypothesis that local diversity reflects escape of rare, small-stature species from dominant, large-stature species in space or time (‘‘fugitive’’ or ‘‘peripheral species’’ concepts; Horn and MacArthur 1972; Keddy et al. 2006). Although bunchgrasses undoubtedly exclude individuals of small-stature species from many microsites that they could otherwise occupy, through mechanisms related to space occupancy (positive effect of bunchgrass removal on species richness at the 0.01-m^2 neighborhood scale; Figure 3.1D) or resource-based competition (Tilman 1989), our results suggest that overall effects of bunchgrasses on recruitment limitation are not manifest on larger-scale patterns of diversity. These results are supported by studies of two additional bunchgrass genera in high-diversity pine savannas: Kirkman et al. (2001) found no correlation between dominance of *Aristida* bunchgrasses and species diversity across a productivity gradient; and Roth et al. (2008) found no effect of experimental removal of a dominant *Andropogon* bunchgrass on local species diversity.

The limited effects of bunchgrasses on local biodiversity observed in these studies do not exclude the possibility that dominant guilds negatively affect performance (e.g., fecundity) of smaller-stature species (Brewer 1998) or other large-stature species (Fargione et al. 2003). Intra-guild competition is a likely mechanism explaining coexistence patterns among large-stature grasses (Fargione et al. 2003), but is a less plausible mechanism to explain the coexistence of rare species that encounter one another infrequently in high-diversity communities. As Grubb (1986:222) pointed out: ‘‘It is not that they [rare species] will never have any impact on each

other . . . The point is that the impact will occur so rarely that even species with extremely similar niches may coexist for a long time.'' Future studies examining the importance of intra- vs. interguild interactions and their consequences on population performance will deepen our understanding of these additional aspects of niche assembly in high-diversity communities.

Species coexistence (or lack thereof) in the face of competition from dominant guilds may be explained by several key functional traits. Rosette-forming forbs can maintain photosynthetic rates and positive carbon balance under the dense canopy of grasses (Walker and Peet 1983). In addition, recruitment from the soil seed bank may allow some species to germinate and increase in biomass before dominant species mature. For example, many of the small-stature species that were abundant under the shrub canopies in our study were seed-banking annuals that reproduce quickly after fire and before shrubs attain maximum size. Spatially extensive, large-stature shrubs, in contrast, may lower diversity by creating a barrier that limits seed dispersal into the interior of shrub patches, killing competitors via increased flammability during fire (Zedler 1995) and via a suite of other competitive traits (Grime 1973). The size-asymmetric effects of shrubs on groundcover forbs and other small-stature species observed in our study parallel patterns observed in other savannas worldwide, where species coexistence reflects niche partitioning between large-stature trees and ''smaller-stature'' grasses (Sankaran et al. 2004). Similarly, in closed-canopy forests, dense understories of large-stature shrubs limit recruitment opportunities for seedlings that may reduce tree species diversity (e.g., Beckage et al. 2005).

Conclusions

The importance of niche and dispersal assembly mechanisms in ecological communities remains a central question in community ecology (e.g., Chase 2003; Leibold et al. 2004; Holyoak et al. 2006). Here, we develop and test key predictions on how two components of these processes

influence the assembly of high-diversity communities, using parallel immigration experiments involving two dominant guilds in exceptionally species-rich pine savannas. We show that immigration by rare, small-stature species enhances local biodiversity, but that the importance of this mechanism depends on the strength of local niche assembly involving competition from some, but not all, dominant guilds. Our study contributes to a broader understanding of how niche- and dispersal-based mechanisms of community assembly vary in their importance in communities of contrasting diversity and suggests that stochastic models of community assembly require some degree of partial determinism to adequately explain biodiversity in species-rich communities.

CHAPTER 4. SEED ARRIVAL, ECOLOGICAL FILTERS, AND PLANT SPECIES RICHNESS: A META-ANALYSIS*

INTRODUCTION

Dispersal plays a central role in a wide range of ecological processes, including community assembly, the maintenance of biodiversity, species coexistence, biological invasions, and ecosystem function (Chase 2003; Levine and Murrell 2003; Stachowicz and Tilman 2005; Zobel et al. 2006). One of the first models to invoke a direct role for dispersal as a key determinant of local biodiversity was MacArthur and Wilson's (1967) Theory of Island Biogeography. A fundamental prediction of this theory is that island species richness should be positively related to rates of immigration from mainland species pools. This seminal work set the stage for "regional" hypotheses of community diversity, which postulate that local communities in species-rich regions should have higher diversity than communities in species-poor regions (Ricklefs 1987; Taylor et al. 1990; Cornell and Lawton 1992; Eriksson 1993; Zobel 1997). These concepts helped to lay the foundation for the burgeoning field of metacommunity ecology (Leibold et al. 2004). In particular, neutral models of biodiversity have invoked a strong role for immigration as one of the main determinants of local biodiversity (Bell 2000; Hubbell 2001). In many of these models, local diversity is primarily controlled by immigration from the broader geographical species pool. In contrast, other models propose that "ecological filters" imposed by local biotic and abiotic conditions influence dispersal-diversity relationships (Elton 1958; Grime 1979; Keddy 1992; Diaz et al. 1998; Huston 1999; Davis et al. 2000; Mouquet and Loreau 2003; Leibold et al. 2004). The extent to which these filters interact with species pools has implications

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for understanding community assembly and biodiversity conservation in the face of habitat loss, fragmentation, and climate change.

Despite widespread interest in the role of dispersal in community assembly, we still lack a synthetic empirical understanding of how species pools and ecological filters interact to structure local biodiversity. To date, experimental tests of the role of propagule supply in natural communities have largely focused on terrestrial plants, with a concurrent growing number of experiments in animal and microbial communities (e.g., Cadotte 2006; Lee and Bruno 2009). In plant populations, there is strong evidence for propagule limitation (Eriksson and Ehrlen 1992; Turnbull et al. 2000; Moles and Westoby 2002; Clark et al. 2007). In a meta-analysis of 159 plant species, Clark et al. (2007) found that populations of most species examined were seed limited, especially in disturbed microsites. Although these patterns suggest an important role for propagule supply at the population level, they do not necessarily scale-up to predictable community-level consequences. For example, increased propagule supply could result in decreased or unchanged local diversity if immigrating species were to outcompete resident species for limiting space or resources. In contrast, propagule arrival could increase species diversity if immigrating species were to recruit into sites unoccupied by resident species or were to promote recruitment of other species. In a combined meta-analysis of nine plant and 28 animal experiments, Cadotte (2006) found support for the hypothesis that dispersal increases mean local diversity. Among plant studies, however, there was no relationship between local species diversity and dispersal, possibly owing to the small number of experiments used in the analysis and/or because only one predictor variable (dispersal rate) was examined. Collectively, these studies underscore the need to better understand the mechanistic consequences of propagule supply at the community level, especially the extent to which propagule arrival interacts with ecological filters to structure local biodiversity.

Ecological filtering occurs when biotic or abiotic factors limit the membership of species in a local community. Biotic filters, notably competition and predation, can influence effects of dispersal on local diversity in at least two important ways. First, increased immigration can reduce local diversity by introducing competitively dominant species or generalist predators into local sites or communities (Mouquet and Loreau 2003). Coexistence of competitively dominant and inferior species can occur, however, if competitively dominant species are dispersal limited (i.e., via "competition-colonization trade-offs;" Tilman 1994), if competitively inferior species disperse short distances to take advantage of nearby sites before dominant species arrive ("spatial successional niches;" Bolker et al. 2003), or if rates of competitive exclusion are delayed owing to community wide recruitment limitation (inferior species win sites by forfeit; Hurtt and Pacala 1995). Second, increased immigration may have no effect on diversity if local communities are "saturated" with species. Here, invasion of diverse local communities may be reduced because of more intense competition for limiting resources (Elton 1958).

Abiotic filters are hypothesized to impose strong constraints on local species membership. Classic examples include models of community diversity proposed by Grime (1979) and Huston (1999), in which the importance of species pools in structuring diversity is influenced by productivity. This "shifting limitations hypothesis" (Foster et al. 2004) predicts that diversity is mostly limited by immigration from species pools at intermediate productivity, whereas establishment limitation imposed by competition for limiting resources becomes more important at high productivity. These concepts have given rise to the idea that community invasibility depends on the dynamics of resource availability (e.g., the "fluctuating resource hypothesis;" Davis et al. 2000), in which invasion is more likely when processes such as disturbance increase space and resources for colonizing species. Disturbance can function both as an ecological filter (e.g., by directly removing resident species from local communities) or as

a process that influences the intensity of other ecological filters (e.g., by altering limiting resources). In this way, locally patchy disturbance can promote coexistence of competing species by increasing "niche dimensionality" within local communities (Harpole and Tilman 2007). In addition, the ability of species to exploit heterogeneity in resources may also depend on "species pool dimensionality" (Questad and Foster 2008), i.e., the diversity of functional groups and traits present in the potential species pool. These ideas have led to the general hypothesis that "species diversity will be greatest in communities with the most environmental heterogeneity, minimal dispersal limitation, and a functionally diverse species pool (Questad and Foster 2008)."

We present a meta-analysis that synthesizes results from 28 studies encompassing 62 experiments that explores how propagule supply (seed arrival) interacts with ecological filters to structure local plant species richness. We tested three main hypotheses. First, we tested whether seed arrival increases local species richness across experiments that did not manipulate the intensity of ecological filters. Second, we tested whether the effect of seed arrival on local species richness was positively related to species-pool diversity, measured in terms of both species diversity (richness and evenness) and functional diversity (functional group richness, evenness, and seed-size diversity) within the pool of species added to local communities in seed-addition experiments. Third, we tested the hypothesis that ecological filters influence the relationship between seed arrival and local species richness. For this hypothesis, we compared the effect of seed arrival under different intensities of ecological filters (owing to disturbance, nutrient availability, or water availability) as well as relationships between local species richness and species-pool diversity in disturbed and undisturbed communities. We show that local species richness is generally limited by seed arrival across a wide range of plant communities. Moreover, we demonstrate that the strength of the positive relationship between seed arrival and species richness is enhanced by disturbance—a pervasive process that strongly influences ecological

filters—as well as species and functional diversity within the pool of arriving seeds. We highlight some empirical gaps that can be addressed by future experiments and discuss the implications of our results for biodiversity theory.

METHODS

We searched the literature using Web of Science (Thompson Reuters) for experiments that manipulated seed arrival in communities and measured plant species richness and/or diversity. Our search included all studies published through December 2008 that contained the keywords "seed addition," "seed sowing," or "seed augmentation," in combination with the keywords "richness" or "diversity." We used the following criteria to select studies for our meta-analysis: (1) sample sizes, means, and standard deviations (or standard errors) for species richness and/or diversity were reported in the paper or provided by the authors on request; (2) experiments contained a control treatment where seed arrival was not manipulated; and (3) the richness and identity of species used in the seed-arrival treatment was known. Most studies reported species richness, but very few reported species diversity or evenness. Therefore, we used species richness as the response variable in our meta-analysis.

We conducted our analysis in MetaWin version 2.0 (Rosenberg et al. 2000) using standard methods described in Gurevitch and Hedges (2001). Following Cadotte (2006), we first calculated an unbiased standardized effect size (Hedge's d) and variance for each experiment (Gurevitch and Hedges 2001). Hedge's d measures the mean difference in the response (species richness) between experimental and control treatments, standardized by the pooled standard deviation and adjusted for small sample size. Most studies did not report means and standard deviations (or standard errors) in the text or tables. For these studies, we used graphical software (DataThief III Version 1.5; http:// datathief.org/) to extract these summary statistics from figures. Some studies used two levels of seed addition (control, addition), whereas others varied the

number of species and/or seed densities added using several treatment levels (Table 4.1). For the latter studies, we used results from the treatment with the highest species richness and density of added seeds. Similarly, when studies used multiple treatment levels for an ecological filter (e.g., nutrient addition), we used results from the highest treatment level. When results were reported for multiple sampling dates in a single paper or in separate papers, we used results from the most recent date or paper. To test hypothesis 1 (seed arrival increases local species richness), we used a mixed-effects model (Gurevitch and Hedges 2001) to calculate a combined mean effect size and 95% confidence interval (CI) for 32 experiments that did not manipulate the intensity of ecological filters. We rejected the null hypothesis if the 95% CI did not overlap zero.

We tested hypothesis 2 (local species richness is positively related to species and functional diversity within the pool of species added to local communities) using continuous, mixed-effects models (i.e., weighted regressions). For each of our five continuous measures of species-pool diversity (species richness, species evenness, functional group richness, functional group evenness, and seed-size diversity; see below), we tested whether the slope of the relationship between effect size and each variable was significantly different from zero based on *P*-values for the between-class homogeneity statistic Q_B (Gurevitch and Hedges 2001). For this analysis, we used data from 17 control experiments in studies that manipulated disturbance (i.e., undisturbed communities) to later compare to results from disturbed communities (see hypothesis 3 below). The results based on these 17 experiments were similar to results based on 29 experiments that did not manipulate ecological filters; for simplicity, we do not present the latter. We used the Dunn-Sidak method (Gotelli and Ellison 2004) to adjust the Type 1 error rate (α) based on five tests each for undisturbed (hypothesis 2) and disturbed (hypothesis 3, below) communities. However, we note that adjustments for multiple comparisons did not change the overall qualitative results. For significant regressions, we calculated the proportion of variation

Table 4.1. Twenty-eight studies testing effects of seed arrival and its interaction with ecological filters on plant species richness.

Study	Habitat	Location	Seed treatment*	*n* spp†	*n* seeds/m^2/year‡		*n* exp§	Ecological filter variables (*n* exp)¶
					Median	Total		
Brown & Fridley (2003)	grassland	USA-NC	density, sr	30	1777	53333	1	.
Dickson & Foster (2008)	grassland	USA-KS	addition	49	300	14700	4	disturbance (1) nutrient (1) water (1)
Eskelinen & Virtanen (2005)	mountain	Finland	addition	14	3200	44800	2	disturbance (1) predation
Foster & Dickson (2004)	grassland	USA-KS	addition	32	400	12800	3	disturbance (1) water (1)
(2004)	grassland	USA-KS	addition	34	400	13600	2	disturbance (1) productivity
Foster & Tilman (2003)	savanna	USA-MN	addition	23	274	43317	1	.
Fraser & Madson (2008)	grassland	USA-OH	addition	20	150	3000	1	predation
Houseman & Gross (2006)	grassland	USA-MI	sr	45	1600	122700	1	productivity
Kalamees & Zobel (2002)	grassland	Estonia	removal	.	.	.	1	competition
Kellogg & Bridgham (2004)	wetland	USA-IN	addition	28	.	.	2	disturbance (1) predation
Klanderud & Totland (2007)	mountain	Norway	sr	27	3019	93225	1	temperature
Lord & Lee (2001)	wetland	USA-NH	addition	8	.	.	3	disturbance (2)
MacDougall & Wilson (2007)	grassland	Canada	density	5	7500	37500	4	disturbance (2) nutrient (1) predation
Mouquet et al. (2004)	grassland	France	addition	8	2775	92841	1	.
Myers & Harms (2009a)	savanna	USA-LA	addition	38	200	11980	4	disturbance/competition (2)
Myers & Harms (unpub. data)	savanna	USA-LA	addition	31	200	9300	3	disturbance (1) water (1)
Paine & Harms (2009)	rainforest	Peru	density, sr	8	3	24	1	.
Questad & Foster (2008)	grassland	USA-KS	addition	13	150	1950	2	disturbance (1)
Reynolds et al. (2007)	grassland	USA-MI	addition	46	842	83014	4	disturbance (1) nutrient (1)
Russell & Roy (2008)	grassland	USA-KS	addition	18	320	5760	3	.
Stein et al. (2008)	grassland	Germany	addition	60	300	14800	1	productivity
Stevens et al. (2004)	grassland	USA-PA	addition	30	1739	235165	3	disturbance (1) nutrient (1)
Suding & Gross (2006)	grassland	USA-MI	addition	22	935	63017	2	disturbance (1)
Tilman (1997)	savanna	USA-MN	sr	54	2931	1323575	1	.
Wilsey & Polley (2003)	grassland	USA-TX	addition	20	2111	80971	4	disturbance (2)
Xiong et al. (2003)	wetland	England	addition	18	400	9600	4	disturbance (2) water (1)
Zobel et al. (2005)	grassland	Estonia	addition	25	1040	26000	1	.
Zobel et al. (2000)	grassland	Estonia	addition	15	1500	22500	2	disturbance (1)

[*]addition = seed-addition experiment where species were added to plots at a single density; density = seed-addition experiment where species were added to plots at varying densities; sr = seed-addition experiment where species were added to plots at different levels of species richness; removal = flowers clipped around plots to reduce seed rain

[†]Maximum number of species added in seed-addition experiments

[‡]Median number of seeds/species and total number of seeds added in seed-addition experiments

[§]Total number of experiments used in the meta-analysis

[¶]Numbers in parentheses indicate the number of experiments used to test the ecological filter hypothesis (hypothesis 3); some filters and experiments could not be used because the requisite data were not available or because of low sample size. Ecological filter variables: disturbance = disturbance manipulated through reduction of total plant cover and/or litter and/or increased soil disturbance; disturbance/competition = disturbance manipulated by removing guilds of competitors; nutrient = fertilization; predation = predators excluded with cages; productivity = study conducted across a natural productivity gradient; temperature = temperature increased; water = irrigation, experimental drought, or natural water gradient.

explained by the model (i.e., r^2) by dividing Q_B (heterogeneity explained by the model) by Q_T (total heterogeneity) (M.S. Rosenberg, *personal communication*).

For each species added as seed in each study, we extracted the seed mass, numbers of seeds added, and/or the total mass of seeds added. We excluded the one study conducted in a forest (Paine and Harms 2009) because the seed densities (24 seeds/m^2) and species added (all woody species) were considerably different than those added in the other studies, all of which were conducted in communities dominated by herbaceous species ($\geq$1950 seeds added/m^2) (Table 4.1). For many studies, we obtained seed mass data from the literature or the Royal Botanic Gardens Seed Information Database (Liu et al. 2008), which we then used to convert the total mass of seeds added for each species to numbers of seeds. To account for differences in plot size among studies, we standardized the number of seeds added per 1 m^2 (Table 4.1). For each experiment, we extracted the species richness of added seeds (Table 4.1) and calculated the species evenness of added seeds using Simpson's evenness (Magurran 2004). We quantified functional diversity in two ways. First, we calculated functional group richness and evenness for species grouped into six standard functional types: non-legume forbs, legume forbs, C_3 grasses, C_4 grasses, woody, and "other graminoids" (sedges and rushes). Second, we calculated functional diversity of seed mass using FD_{var} (Mason et al. 2003). This index measures the variation in a functional trait weighted by species' abundances, is unaffected by species richness in the sample, and ranges from 0 to 1 (Mason et al. 2003). We will refer to this measure generally as "seed-size diversity."

We tested hypothesis 3 (ecological filters influence the relationship between seed arrival and local species richness) in two ways. First, we used categorical, mixed-effects models to test for differences in mean effect size between control and treatment groups within studies that manipulated the intensity of ecological filters (Table 4.1). We performed separate analyses for

three ecological filter variables for which requisite data were available from ≥ 4 experiments: disturbance (n = 19–21), nutrient availability (n = 4), and water availability (n = 4). Our disturbance category includes experiments that manipulated microsite availability either directly (e.g., manual removal of biomass or litter) or indirectly (e.g., fire). Thus, we use disturbance in a broad sense as both an ecological filter, as well as a process that influences the intensity of other ecological filters. Second, we used the weighted regression methods described above to test for positive relationships between effect size and each of the five continuous measures of species-pool diversity in disturbed communities (n = 18 experiments with requisite data); we did not perform regressions for the other ecological filters due to small sample size.

We also examined four additional covariates that could influence effect sizes: (1) study length; (2) plot size; (3) local community richness (mean species richness in control plots); and (4) a potential source of publication bias (ISI journal impact factor; Web of Science). We tested the significance of each continuous variable using the weighted regression methods described above and data from experiments that did not manipulate an ecological filter (n = 29 with requisite data), undisturbed communities (n = 17), and disturbed communities (n = 18).

RESULTS

We found a total of 28 studies encompassing 62 experiments (Table 4.1). Twenty-seven of the studies increased seed arrival through experimental seed addition, whereas one study (Kalamees and Zobel 2002) reduced seed arrival by removing flowers. The median plot size used for experimental treatments was 1 m^2 (range = 0.002–9 m^2). Across seed-addition experiments, the median percentage of added species that were absent from ≥ 1 control (no seed addition) plot was 81% (range = 40–100%; n = 20 studies with available data). Thus, most seed-addition species were likely members of the broader (regional) species pool, although most studies also added members of the local species pool (species occurring naturally in control plots). The

studies spanned a wide range of habitat types (forest, grassland, montane and alpine communities, savanna, and wetland), but most (64%) were conducted in grasslands. Of the 28 studies, 75% examined how seed arrival interacts with one or more ecological filters to influence local species diversity. The most common ecological filter variable examined was disturbance (17 studies), followed by nutrient availability (4), water availability (4), predation (4, 3 of which included requisite controls), productivity (3), and temperature (1).

Hypothesis 1: Seed Arrival Increases Local Species Richness

Seed arrival significantly increased local species richness (Figure 4.1a). Among all 62 experiments, 70% had significantly positive effect sizes (95% CI's did not overlap zero) and only one study had a significantly negative effect size. Among the 32 experiments that did not manipulate an ecological filter, the combined mean effect size was significantly positive (Figure 4.1a).

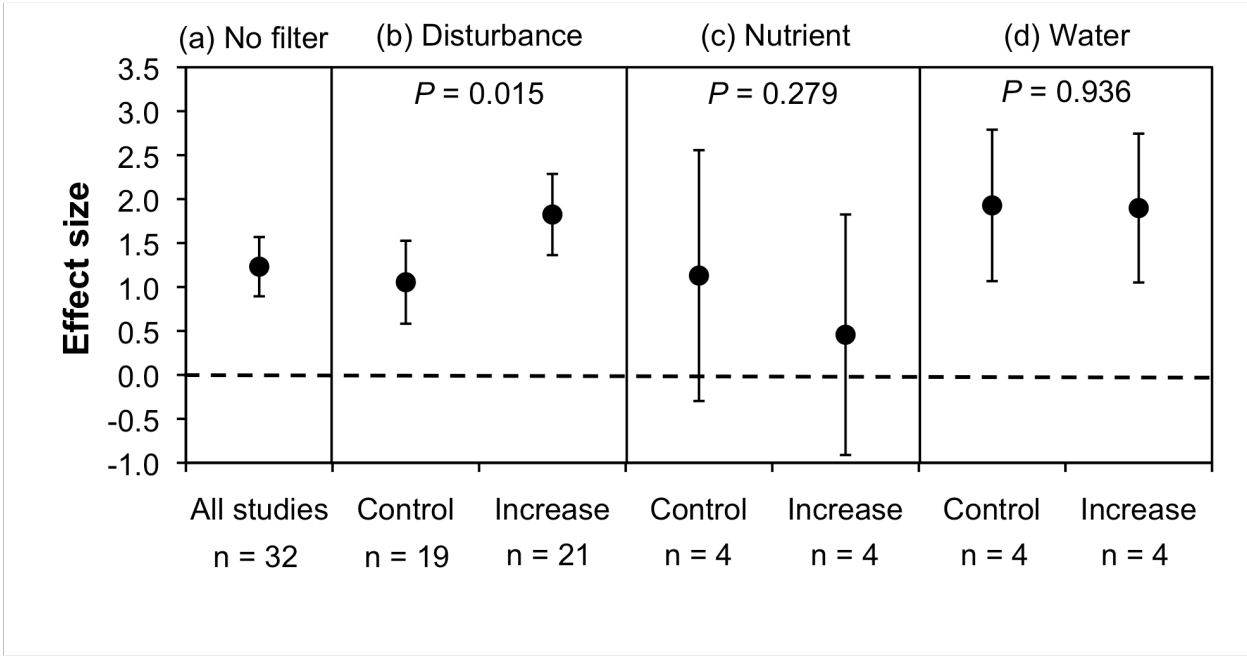

Figure 4.1. Mean effect size (Hedge's $d \pm 95\%$ confidence interval) of seed arrival on local plant species richness (a) in experiments where ecological filters were not manipulated and in response to (b) disturbance, (c) nutrients, and (d) water availability. *P*-values from categorical, mixed-effects models testing for differences in mean effect sizes among control and treatment groups are shown in panels b-d (see Appendix C for homogeneity statistics).

Hypothesis 2: Local Species Richness is Positively Related to Species-pool Diversity

In undisturbed communities, the effect of seed arrival on local species richness was positively influenced by species evenness in the pool of species added in seed-addition experiments (P = 0.0287, $r^2 = 0.26$, $\alpha = 0.05$), but not species richness or functional diversity (richness, evenness, or seed-size diversity; $P \geq 0.220$) in the seed pool (Figure 4.2, top panels; Appendix C). However, the significant relationship between effect size and species evenness became marginally non-significant after adjusting for multiple tests (adjusted α for five tests = 0.01). In summary, we found that local species richness was strongly limited by seed arrival and positively related to species evenness in the seed pool.

Hypothesis 3: Ecological Filters Influence the Seed Arrival-Species Richness Relationship

Seed arrival had a stronger positive effect on species richness in disturbed relative to undisturbed communities (Figure 4.1b; Appendix C). Disturbance significantly increased the mean effect size by 73% (Figure 4.1b; $P = 0.015$; n = 19–21 experiments). In contrast, nutrient addition decreased the mean effect size, but not significantly (Figure 4.1c; $P = 0.279$; $n = 4$ studies). There was also no significant effect of water availability on mean effect size (Figure 4.1d; $P = 0.936$; $n = 4$ studies).

In disturbed communities, effect size was positively related to species evenness and seed-size diversity in the pool of species added in seed-addition experiments (Figure 4.2, bottom panels; Appendix C). Moreover, the positive relationship between effect size and species evenness was stronger in disturbed ($P = 0.0002$, $r^2 = 0.45$) relative to undisturbed ($P = 0.0287$, $r^2 = 0.26$) communities (Figure 4.2). This pattern was further supported by a negative relationship between effect size and the total density of seeds added/m^2/year in disturbed (weighted regression; $P = 0.0004$, $r^2 = 0.43$), but not undisturbed ($P = 0.1009$), communities. In contrast, there were no strong relationships between effect size and species richness ($P = 0.9553$),

functional richness ($P = 0.5136$), or functional evenness ($P = 0.0779$) in the seed pool (Figure 4.2, bottom panels). In summary, local species richness was more strongly limited by seed arrival in disturbed relative to undisturbed communities. In addition, effect size was more strongly related to species evenness, and only related to seed-size diversity, in disturbed communities.

Potential Covariates Influencing Effect Sizes

Across 29 experiments that did not manipulate an ecological filter, we found no relationship between effect size and study length ($P = 0.6600$), plot size ($P = 0.2859$), local community richness ($P = 0.6852$), or journal impact factor ($P = 0.8160$). There were also no relationships between effect size and these variables in undisturbed or disturbed communities (n = 17–18 experiments, $P \geq 0.274$ in all regressions).

DISCUSSION

Propagule Supply and Local Species Richness

Our meta-analysis provides strong support for the hypothesis that local plant species richness is limited by seed arrival from local and regional species pools. We found that seed arrival significantly increased local species richness in a wide range of communities, including forest, grassland, savanna, wetland, and montane communities. All but one of the studies (Kalamees and Zobel 2002) manipulated seed arrival by experimentally adding seeds from local and/or regional species pools, suggesting an important influence for immigration from species pools in local community assembly. Enhancement of local diversity via immigration can be explained by a variety of mechanisms, including the presence of recruitment opportunities (available microsites) in unsaturated communities, satiation of seed and seedling predators (Turnbull et al. 2000), facilitation of immigrating species by resident species (Bruno et al. 2003), and reduction in local extinction owing to mass effects (Leibold et al. 2004). The importance of species pools

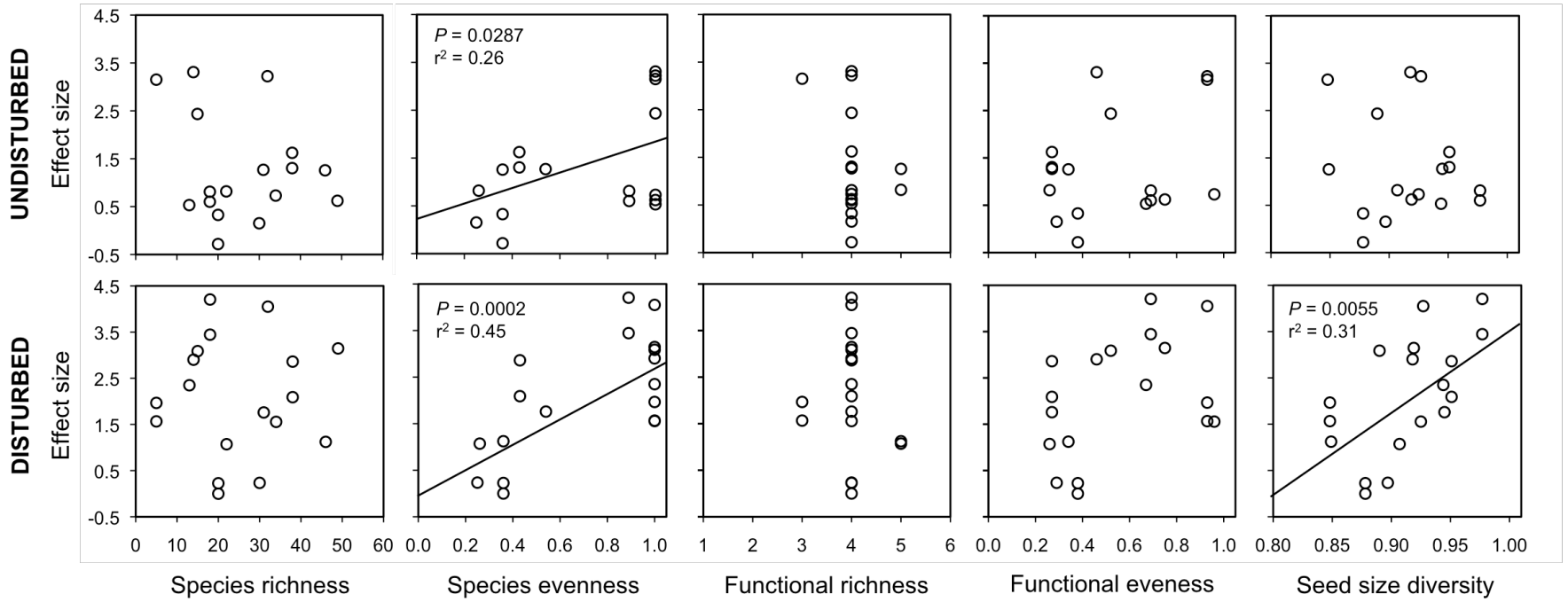

Figure 4.2. Relationship between effect size (Hedge's *d*) and the species richness, species evenness (Simpson's evenness), functional group richness, functional group evenness, and seed-size diversity (FD_{var}) of plant species added to local communities in seed-addition experiments. The relationships are plotted for 17 experiments in undisturbed communities (top) and 18 experiments in disturbed communities (bottom). Summary statistics from weighted regressions are shown for relationships with $P < 0.05$ (see Appendix C for homogeneity statistics).

in structuring local communities is widely recognized (Ricklefs 1987; Taylor et al. 1990; Cornell and Lawton 1992; Eriksson 1993; Zobel 1997; Leibold et al. 2004), but much of the empirical evidence comes from correlative studies of large- and small-scale diversity patterns (e.g., Ricklefs and Schluter 1993; Partel et al. 1996; Caley and Schluter 1997). Even though it is not practical in most situations to manipulate regional species richness and observe the consequences for local species richness, the propagule-arrival experiments summarized here provide useful insights into what happens locally when immigration from, or the size of, species pools increase(s).

We found little evidence for negative effects of seed arrival on local species richness, a pattern inconsistent with competition-colonization trade-off models of species coexistence (e.g., Tilman 1994). A key assumption of these models is that arrival of dominant competitors results in competitive exclusion of resident species, thereby reducing local diversity. The absence of this pattern in our analysis may simply reflect that the duration of most experiments was too short to observe competitive exclusion. Alternatively, propagule arrival and competition may influence components of community structure other than species richness, such as species relative abundance (e.g., Mouquet et al. 2004). In our analysis, most studies only reported species richness, so we were unable to assess treatment effects on species relative abundance and evenness. We advocate that, when possible, future experimental studies decompose effects of propagule supply on species diversity into both species richness and evenness components. The lack of negative effects of immigration on species richness could also be attributed to species selection, i.e., dominant competitors may not have been added to local communities as seed-addition species, or were added at low enough densities to preclude strong competitive effects. This explanation seems less likely, however, given that positive relationships were generally observed within studies that manipulated levels of species richness in the seed-addition pool

(Tilman 1997; Brown and Fridley 2003; Houseman and Gross 2006; Klanderud and Totland 2007) and the large numbers of species (median of 25 species) and seeds (median of >800 seeds/species/m^2) added.

Species-pool Diversity and Ecological Filters

We found that the effects of seed arrival and species-pool diversity on local species richness were positively influenced by three factors: (1) evenness of species in the seed pool; (2) disturbance; and (3) seed-size diversity in the seed pool. Positive effects of seed-pool evenness may reflect a reduction in both local extinctions caused by demographical stochasticity (fewer rare species in the pool) and competitive effects of dominant species or functional groups within the pool. Disturbance increased the mean effect size by 73%, and the positive effects of species evenness and seed-size diversity on local species richness were stronger in disturbed relative to undisturbed communities. These results strongly support the hypothesis that disturbance plays a key role in mediating effects of species pools on local community assembly.

To understand the mechanistic causes and consequences of these patterns, it is important to consider the timing of disturbance relative to the timing of seed arrival. In most of the experiments used in our analysis, disturbance was manipulated prior to seed-arrival treatments. These studies therefore demonstrate an important role for disturbance in reducing post-dispersal establishment limitation imposed by factors such as space limitation, competition for limiting resources, and low niche dimensionality in local communities. Disturbance also influences recruitment from the soil seed bank, which can potentially obscure effects of seed arrival on species richness. In most of the disturbance experiments summarized here, it is not possible to distinguish the relative importance of these mechanisms, although some studies have directly manipulated interspecific competition (Myers and Harms 2009a), seed bank recruitment (Kalamees and Zobel 2002), and niche dimensionality (Questad and Foster 2008).

The positive relationship between species richness and seed-size diversity in disturbed (but not undisturbed) communities supports the hypothesis that species diversity should be highest in communities with environmental heterogeneity and a functionally diverse species pool (Questad and Foster 2008). Questad and Foster (2008) experimentally tested this hypothesis by creating a functionally redundant and functionally complementary species pool and measuring their effects on local plant diversity in the presence and absence of spatio-temporal heterogeneity imposed by disturbance. They concluded that a combination of high species-pool dimensionality (higher functional diversity) and niche dimensionality (environmental heterogeneity) maintained species coexistence by facilitating species sorting in heterogeneous environments. Our general finding of a positive relationship between local species richness and seed-size diversity in disturbed communities is consistent with this idea, suggesting that coexistence via species sorting may be a widespread mechanism in plant community assembly. Seed size is widely recognized as a key functional component of plant ecological strategies linked to species' regeneration niches (Westoby et al. 2002). Higher variation in seed size in the potential species pool can therefore allow more species to exploit "windows of opportunity" (Davis et al. 2000) created when disturbance increases environmental heterogeneity in local communities. Our analysis illustrates the utility of examining functional biodiversity in species pools as a continuous variable measured in terms of a single key trait. Extending this framework by examining multiple functional traits provides a promising avenue for future observational and experimental studies.

Our review highlights the need to better understand how additional ecological filters interact with seed arrival to structure biodiversity. Although a wide range of ecological filters has been examined (related to disturbance, nutrient availability, water availability, competition, predation, productivity, temperature; Table 1), the small number of experiments available for

most ecological filters limits our ability to draw general conclusions. The lack of effects of nutrient or water availability observed in our analysis probably reflected small sample size ($n = 4$ experiments). In contrast, these abiotic filters could have both positive and negative effects on seed and seedling recruitment, resulting in no net effect on species richness. Of the three studies that examined effects of productivity and seed arrival on local species richness (Foster et al. 2004; Houseman and Gross 2006; Stein et al. 2008), all demonstrated an interaction between the two factors, whereby positive effects of seed arrival declined at high productivity. These studies provide support for the shifting limitations hypothesis (Foster et al. 2004) based on the models of Grime (1979) and Huston (1999). Finally, we second the call by Turnbull et al. (2000) for more experiments addressing the interactive effects of natural enemies (e.g., seed predators) and seed limitation on plant populations and their community-level consequences. In the studies we examined, some natural enemies positively affected recruitment of dispersing species by reducing plant biomass and competition (Eskelinen and Virtanen 2005), whereas others negatively affected dispersing species via seed predation (Fraser and Madson 2008). Future experiments that disentangle effects of natural enemies can help to clarify the conditions under which propagule arrival influences biodiversity.

Where Do We Go from Here? Limitations and Empirical Gaps

Natural Levels of Seed Rain

An important limitation of most current seed-addition experiments is that natural levels of seed rain are not reported or unknown (Turnbull et al. 2000; Clark et al. 2007). To our knowledge, the highest level of seed rain reported for grasslands is 19700 seeds/m^2/year (North-American tall-grass prairie; Rabinowitz and Rapp 1980), and numbers are known to vary widely among communities (e.g., 3820–10 000 seeds/m^2/year in European grasslands; Poschlod and Jordon 1992; Jakobsson et al. 2006). Among the studies included in our review, 50% used total seed

densities that exceeded 20000 seeds/m^2/year and 39% used densities exceeding 40000 seeds/m^2/year, i.e., more than double the seed rain reported by Rabinowitz and Rapp (1980). High seed densities are useful when the goal of the experiment is to saturate most microsites with seeds or if seed viability is especially low, although seed viability data are infrequently reported. However, adding seeds at densities that occur well outside natural levels of seed rain can result in an overestimate of the importance of species pools in limiting observed local diversity. In addition, most studies added seeds in a single dispersal event, thereby removing interspecific differences in the timing of dispersal, a process that can have important influences on community assembly. Although studies of natural seed rain may require significant investments in time, resources, and the selection of appropriate seed traps (e.g., Chabrerie and Alard 2005), they will greatly improve both the design and interpretation of seed-addition experiments.

The Role of Dispersal in Species Coexistence vs. Diversity Limitation

The relative roles of dispersal in limiting vs. maintaining community diversity has received little attention, but has important implications for understanding community assembly, species coexistence, and biodiversity patterns at multiple scales (Vandvik and Goldberg 2005, 2006). Vandvik and Goldberg (2005, 2006) suggested an approach that partitions diversity into components that are independent of, maintained by, or limited by dispersal. This distinction is important, because it helps to clarify differences in the way dispersal has been conceptualized in the literature, e.g., in spatial models of species coexistence (Amarasekare 2003; Levine and Murrell 2003) vs. models based on dispersal limitation from regional species pools (e.g., MacArthur and Wilson 1967; Hubbell 2001). In this context, the seed-addition experiments used in our analysis generally provide insight into the extent to which community diversity is limited by dispersal (i.e., immigration; Vandvik and Goldberg 2005). In contrast, seed-arrival experiments that directly manipulate seed shadows are better suited towards understanding how

dispersal maintains species coexistence (Stoll and Prati 2001; Levine and Murrell 2003). The utility of these complementary approaches does not necessarily reflect processes operating at different spatial scales. For example, metacommunity models predict that arrival of dominant competitors from the regional species pool reduces local diversity (Leibold et al. 2004). To resolve the general question of how dispersal facilitates species coexistence and limits diversity, we need better empirical data on several fronts, including the extent to which dispersal limitation differs among species (Clark 2009), interspecific trade-offs between dispersal ability and other ecological traits (Levine and Murrell 2003), functional mechanisms influencing interspecific responses to ecological filters, and how stochasticity in propagule arrival influences community assembly (Chase 2003; Turnbull et al. 2008).

Conclusions

Our review of experimental studies indicates that local plant species richness is generally limited by propagule supply, and that the consequences of propagule arrival for local diversity can be strongly influenced by ecological filters, such as those mediated by disturbance. Three important implications emerge from our meta-analysis. First, current experimental studies in plant communities suggest a fundamental role for species pools in local community assembly, species coexistence, and biodiversity. Positive effects of species pools on local biodiversity suggest that many communities are unsaturated with species and open to invasion by both native and exotic species. At the same time, propagule supply imposes a strong limit to local diversity that can potentially have cascading effects on community stability (e.g., increased local extinctions) and ecosystem function (e.g., changes to primary productivity; Zobel et al. 2006; Lee and Bruno 2009). Second, a comprehensive understanding of the role of dispersal-based processes in community ecology will require synthetic approaches that explore how dispersal and environmental heterogeneity interact to structure communities. Theoretical and empirical

contributions in this area will become increasingly important in the face of global environmental change owing to rapid habitat loss, fragmentation, and climate change. Finally, we need more empirical studies that test the mechanisms proposed to explain dispersal-diversity patterns, including the importance of functional trait diversity in local and regional species pools. The experimental studies reviewed here provide a useful framework from which we can build and expand on to help reconcile many outstanding questions in community ecology.

CHAPTER 5. CONCLUSIONS

SUMMARY OF KEY RESULTS

My dissertation makes several contributions towards our mechanistic understanding of community assembly and the maintenance of local biodiversity. First, my experiments and meta-analysis provide strong support for the hypothesis that local plant species diversity is strongly limited by dispersal in high-diversity pine savannas (Chapters 2 and 3) and a wide range of plant communities (forest, grassland, montane, savanna, wetland) (Chapter 4). These results suggest that many plant communities are not saturated with species and open to invasion from local and regional species pools. Second, my experiments support the hypothesis that niche-based ecological filters limit the extent to which community assembly is influenced by dispersal from the species pool. In high-diversity pine savannas, the positive effects of dispersal on local diversity were reduced by changes in soil moisture, following low-intensity fire that opens less space and removes less biomass than high-intensity fire (Chapter 2), and in the presence of competition from some, but not all, dominant guilds (Chapter 3) (Table 5.1). Moreover, local communities assembled in the presence of strong ecological filters (high-intensity fire and high soil moisture) were more similar in species composition than communities assembled in the absence of those filters (Table 5.1), illustrating conditions that may reduce stochastic community assembly (Chapter 2). These results provide insights into the ecological conditions that influence the position of high-diversity plant communities along the niche-dispersal assembly continuum in space (e.g., spatially variable fire intensities and competitive neighborhoods) and time (e.g., in drought and high-rainfall years). Finally, my meta-analysis showed that dispersal had a stronger positive effect on local species richness in disturbed relative to undisturbed plant communities, and when the species pool contained high species diversity and functional-trait diversity,

supporting the general hypothesis that plant-community assembly reflects a dynamic interplay between species-pool diversity and local environmental heterogeneity (Chapter 4).

A CONCEPTUAL MODEL OF COMMUNITY ASSEMBLY IN HIGH-DIVERSITY PINE SAVANNAS

My results and ongoing research suggest a mechanistic conceptual model for community assembly in longleaf pine savannas, with broader implications for understanding the assembly of other high-diversity plant communities and communities of contrasting diversity (Figure 5.1). I propose that two conditions generally contribute to stochastic community assembly in high-diversity pine savannas. First, because most species in these communities are rare (e.g., Keddy et al. 2006), population sizes and local diversity should generally be recruitment limited. This prediction is strongly supported by my experiments: local diversity was strongly limited by seed arrival regardless of local fire intensity, soil moisture, and competition from dominant guilds (Chapters 2, 3). Pervasive recruitment limitation at the community level slows deterministic competition exclusion (Hurtt and Pacala 1995), thereby increasing the probability that stochastic processes such as chance colonization influence community assembly (Figure 5.1). Second, communities assembled from a large species pool should be more strongly influenced by the history of seed arrival and priority effects relative to communities assembled from a smaller species pool (Chase 2003). These two conditions will tend to increase the importance of dispersal assembly relative to niche assembly in high-diversity longleaf pine savannas (Figure 5.1) and other species-rich plant communities that harbor large numbers of rare species and a large regional species pool.

Although stochastic processes may generally play an important role in the assembly of high-diversity communities (Sale 1977; Hubbell and Foster 1986; van der Maarel and Sykes 1993; Hurtt and Pacala 1995; Hubbell 2001), I propose that the importance of stochastic

Table 5.1. Summary of experimental effects of three niche-based ecological filters on local communities and populations in a high-diversity longleaf pine savanna. The dashed box indicates untested predictions.

Ecological filter	Effect of ecological filter on local communities and focal seed-addition species					
	Species richness	Positive effect of dispersal on species richness	Total recruitment from the species pool[1]	Community similarity	Total aboveground biomass	Growth and population size of focal species[2]
1. Locally intense fire	decrease	increase	increase	increase	decrease	increase
2. Soil moisture						
Low	decrease	decrease	decrease	no effect or increase	decrease	decrease
High	decrease	decrease	increase	increase	no effect	increase or decrease
3. Competition						
Bunchgrass	no effect	no effect	no effect	no effect	decrease	decrease
Shrub	decrease	no effect	decrease	increase	decrease	decrease

[1]Total density of focal seed-addition species

[2] Results refer to most (but not all) focal seed-addition species examined (J.A. Myers and K.E. Harms, *unpublished data*)

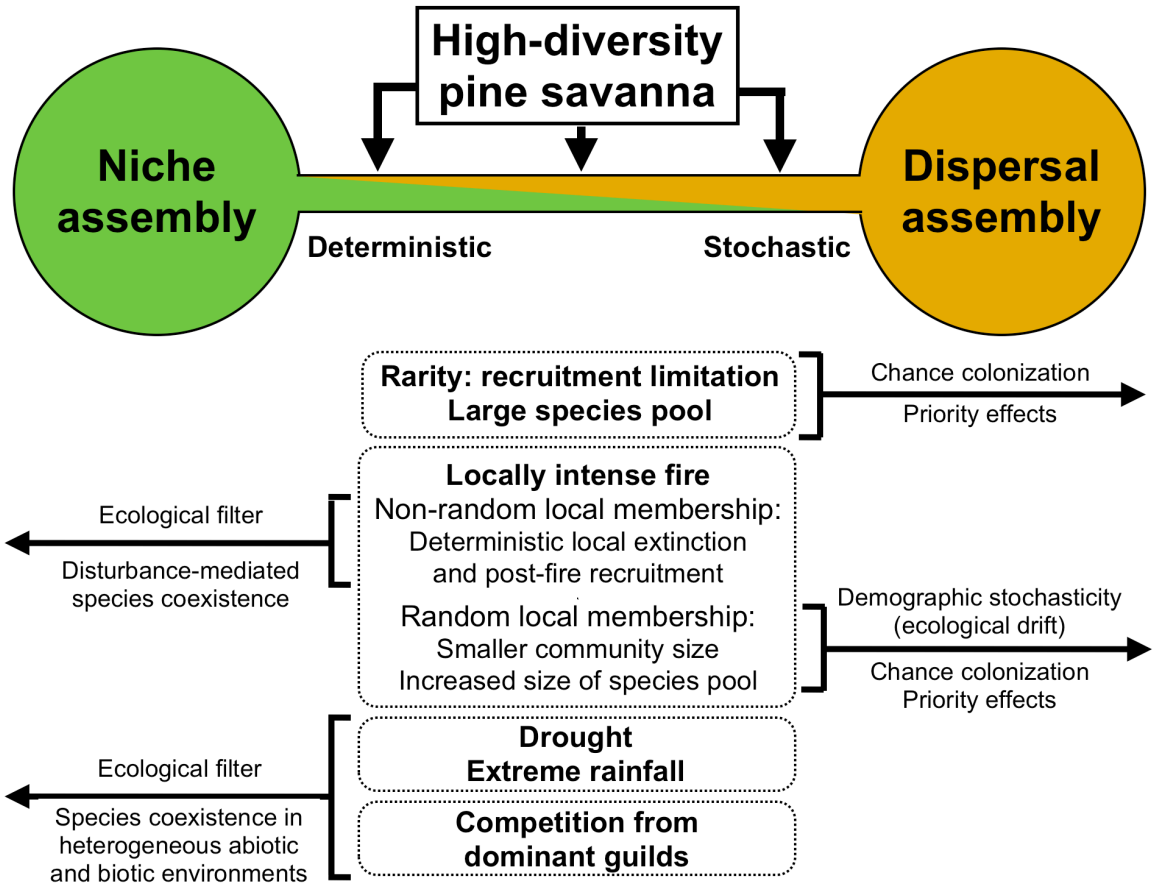

Figure 5.1. A conceptual model of community assembly in high-diversity longleaf pine savannas. In high-diversity communities, rarity and a large species pool can both increase the importance of stochastic processes in community assembly. However, the importance of stochastic processes can be reduced under conditions in which niche-based ecological filters deterministically limit local species membership. These filters can also contribute to species coexistence when they are heterogeneous in space (e.g., local fire intensity; competition) or time (e.g., rainfall).

community assembly may vary in space and time in high-diversity plant communities, depending on the presence and strength of niche-based ecological filters (Figure 5.1; see also Chase 2007). My results suggest that abiotic and biotic ecological filters may decrease the importance of stochastic community assembly via their deterministic effects on both established species as well as on species that arrive as seeds from the species pool (Figure 5.1). I found that high-intensity fire, changes in soil moisture, and competition from at least one dominant guild (large-stature shrubs) reduced local species richness (Table 5.1). Importantly, local fire intensity and soil

moisture modified the effects of dispersal on species richness and recruitment from the species pool (Table 5.1). If these changes in biodiversity are non-random with respect to species and their functional traits, then these ecological filters will tend to increase the importance of niche-based community assembly (Figure 5.1). This prediction is partially supported by the difference in community similarity (i.e., beta diversity) I observed in communities assembled under contrasting fire intensity and soil moisture (Table 5.1). My ongoing research suggests that these patterns at the community level may be influenced by growth rates of individuals and populations of some small-stature forbs in response to changes in resource availability (e.g., increased space following high-intensity fire and reduced soil moisture under drought conditions) (Table 5.1). These population-level processes may contribute to species coexistence in heterogeneous environments (Chesson 2000), but it remains unclear how much these processes matter for species coexistence relative to stochastic processes in high-diversity communities.

Locally intense fires may also contribute to both deterministic and stochastic community assembly (Figure 5.1). My results suggest that high-intensity fire can decrease the importance of stochastic community assembly both by functioning as a niche-based abiotic filter that deterministically excludes species from local communities, as well as by processes that reduce the effects of other ecological filters (e.g., competition for space and other resources), thereby increasing recruitment from the species pool (e.g., recruitment of gap-dependent species). In contrast, high-intensity fire may also contribute to stochastic community assembly in two ways. First, high-intensity fire may contribute to ecological drift by decreasing the size of local communities: reduced population sizes of many species following high-intensity fire will be more prone to local extinction owing to demographic stochasticity. In this way, fire may function in a way analogous to generalist predators in the assembly of prey communities (Chase et al.

2009). Second, by increasing space and other resources, high-intensity fire may increase the size of the potential species pool from which local communities can be assembled. A larger potential species pool, in turn, will further increase the probability that immigration history and priority effects influence community assembly. I hypothesize that the net effect of high-intensity fire on deterministic vs. stochastic community assembly will depend on: (1) the extent to which biodiversity loss from high-intensity fire and biodiversity gains from post-fire recruitment are non-random with respect to species and their functional traits; and (2) the species diversity and functional diversity of the species pool from which post-fire communities are assembled.

My conceptual model can be extended to make predictions for how the effects of ecological filters vary across soil-moisture gradients, as well as synergistic effects of some ecological filters. Soil-moisture is one of the principal factors influencing species diversity and composition in the longleaf pine ecosystem (e.g., Peet and Allard 1993). In extremely dry communities, I hypothesize that large openings in the groundcover created by locally intense fire may have a net negative effect on local biodiversity if plant cover is required to facilitate recruitment under drought conditions. In contrast, at extremely wet and more productive sites, locally intense fire may have a net positive effect on local biodiversity by reducing local competitive exclusion. High-intensity fire may therefore contribute to niche assembly in both dry and wet communities, but the underlying mechanisms may differ among those communities. Because large-stature bunchgrasses dominate the groundcover plant community, I also hypothesize that the effects of bunchgrasses on local diversity may shift from neutral or negative in wet communities to positive (i.e., facilitation) in dry communities. In addition, increased soil moisture in high-rainfall years should have a strong positive effect on local diversity in dry communities (i.e., strong effects on niche assembly), but neutral or negative effects in wet communities with saturated soil conditions (weaker effects on niche assembly). Finally, my

ongoing research suggests that soil moisture and local fire intensity have synergistic effects on population and community dynamics, e.g., when soil-moisture history in a local community influences the effects of high-intensity fire on local extinctions and biodiversity. These results have implications for understanding how feedbacks between climate change (e.g., increased droughts and extreme rainfall) and fire disturbance may influence community assembly.

IMPLICATIONS FOR BIODIVERSITY THEORY AND CONSERVATION

The relative importance of niche- and dispersal-assembly theory in explaining biodiversity remains one of the most central and unresolved issues in ecology. Many theoretical and empirical studies have viewed these general theories as dichotomous and opposing explanations for biodiversity patterns. In contrast, recent studies have moved towards a more synthetic view, whereby these general theories mark the extreme endpoints of a continuum of hypotheses to explain biodiversity (e.g., Tilman 2004; Gravel et al. 2006; Chase 2007; Figure 1.1). My dissertation contributes to this synthesis by providing a conceptual framework for understanding the conditions in which niche and dispersal assembly contribute to the maintenance of biodiversity in high-diversity plant communities (Figure 5.1). I propose that a synthetic model of community assembly in longleaf pine savannas, and other high-diversity plant communities, should explicitly consider three fundamental factors: (1) the consequences of rarity and pervasive recruitment limitation in contributing to stochastic community assembly; (2) the consequences of large regional species pools on stochastic community assembly; and (3) the effects of niche-based ecological filters in reducing the importance of stochastic community assembly in space and time. Importantly, this conceptual framework can be extended to understand the assembly of communities with contrasting diversity, e.g., using comparative studies of community assembly in communities with large vs. small numbers of rare species and communities assembled from a large vs. small regional species pool (e.g., Chase 2003).

My results also have implications for restoration and conservation of threatened longleaf pine communities. Today, most remnant longleaf pine communities exist in a fragmented landscape and are largely isolated from one another (e.g., Keddy et al. 2006). Restoration and biodiversity conservation in these fragments require prescribed fire, and in many cases, reintroduction of plant species from the regional species pool using seed introductions (Walker and Silletti 2006). My results suggest that seed introductions are likely to have the largest effect on recruitment and species diversity when seeds are added in years in which sites are burned and rainfall is less likely to limit seed germination and seedling establishment. Moreover, to the extent that the maintenance of diversity is promoted by heterogeneity in local fire intensity, managers could manipulate local fuel loads to create a mixture of post-fire conditions. Synergistic effects involving fire, rainfall, and immigration from the regional species pool will likely play an increasingly important role in the maintenance of biodiversity in the face of climate change (e.g., increased droughts and extreme rainfall), habitat loss (smaller communities and species pools), and fragmentation (reduced dispersal and genetic diversity). Future studies that further disentangle how these ecological processes interact to maintain biodiversity can help guide the restoration and conservation of longleaf pine communities, one of the most endangered and biologically rich ecosystems on earth.

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APPENDIX A. SUPPLEMENTARY MATERIAL FOR CHAPTER 2

Species, Densities, and Viability of Seeds Used in the Dispersal Treatment

Thirty-one species added in the dispersal treatment in 2007, showing dispersal type based on seed morphology, number of seeds added per 0.5-m^2 subplot, and percent seed germination on petri dishes (n = 50 seeds/species; germination was not tested for *H. gronovii*).

Species	Family	Life form[1]	Dispersal type	*n* seeds added	Germination (%)
Ageratina aromatica	Asteraceae	PF	wind	300	94
Carex glaucescens	Cyperaceae	PS	gravity	30	84
C. tenax	Cyperaceae	PS	gravity	30	94
Chromolaena ivifolia	Asteraceae	PF	wind	200	68
Chrysopsis mariana	Asteraceae	PF	wind	30	26
Cirsium horridulum	Asteraceae	BF	wind	50	88
Conoclinium coelestinum	Asteraceae	PF	wind	300	96
Crotalaria purshii	Fabaceae	PL	gravity	25	12
Elephantopus tomentosus	Asteraceae	PF	wind	350	88
Eryngium yuccifolium	Apiaceae	PF	gravity	100	28
Eupatorium album	Asteraceae	PF	wind	50	14
Eupatorium rotundifolium	Asteraceae	PF	wind	200	40
Eurybia paludosa	Asteraceae	PF	wind	50	26
Helenium flexuosum	Asteraceae	PF	gravity	200	86
Helianthus angustifolius	Asteraceae	PF	gravity	100	68
H. radula	Asteraceae	PF	gravity	200	68
Hieracium gronovii	Asteraceae	PF	wind	30	–
Hypericum crux-andreae	Clusiaceae	W	gravity	100	46
H. setosum	Clusiaceae	PF	gravity	200	88
Hyptis alata	Lamiaceae	PF	gravity	500	54
Liatris pycnostachya	Asteraceae	PF	wind	50	28
L. squarrulosa	Asteraceae	PF	wind	75	66
Ludwigia hirtella	Onagraceae	PF	gravity	100	82
Plantago virginica	Plantaginaceae	AF	gravity	30	98
Pycnanthemum albescens	Lamiaceae	PF	gravity	400	16
Rhexia alifanus	Melastomataceae	PF	gravity	50	14
Rhexia mariana	Melastomataceae	PF	gravity	50	64
Rudbeckia hirta	Asteraceae	PF	gravity	200	30
Salvia lyrata	Lamiaceae	PF	gravity	50	62
Solidago odora	Asteraceae	PF	wind	100	84
S. rugosa	Asteraceae	PF	wind	500	36

[1]AF = annual non-legume forb, BF = biennial non-legume forb, PF = perennial non-legume forb, PL = perennial legume forb, PS = perennial sedge, W = woody

ANOVA Tables for Biomass, Soil Moisture, Species Richness, and Total Density

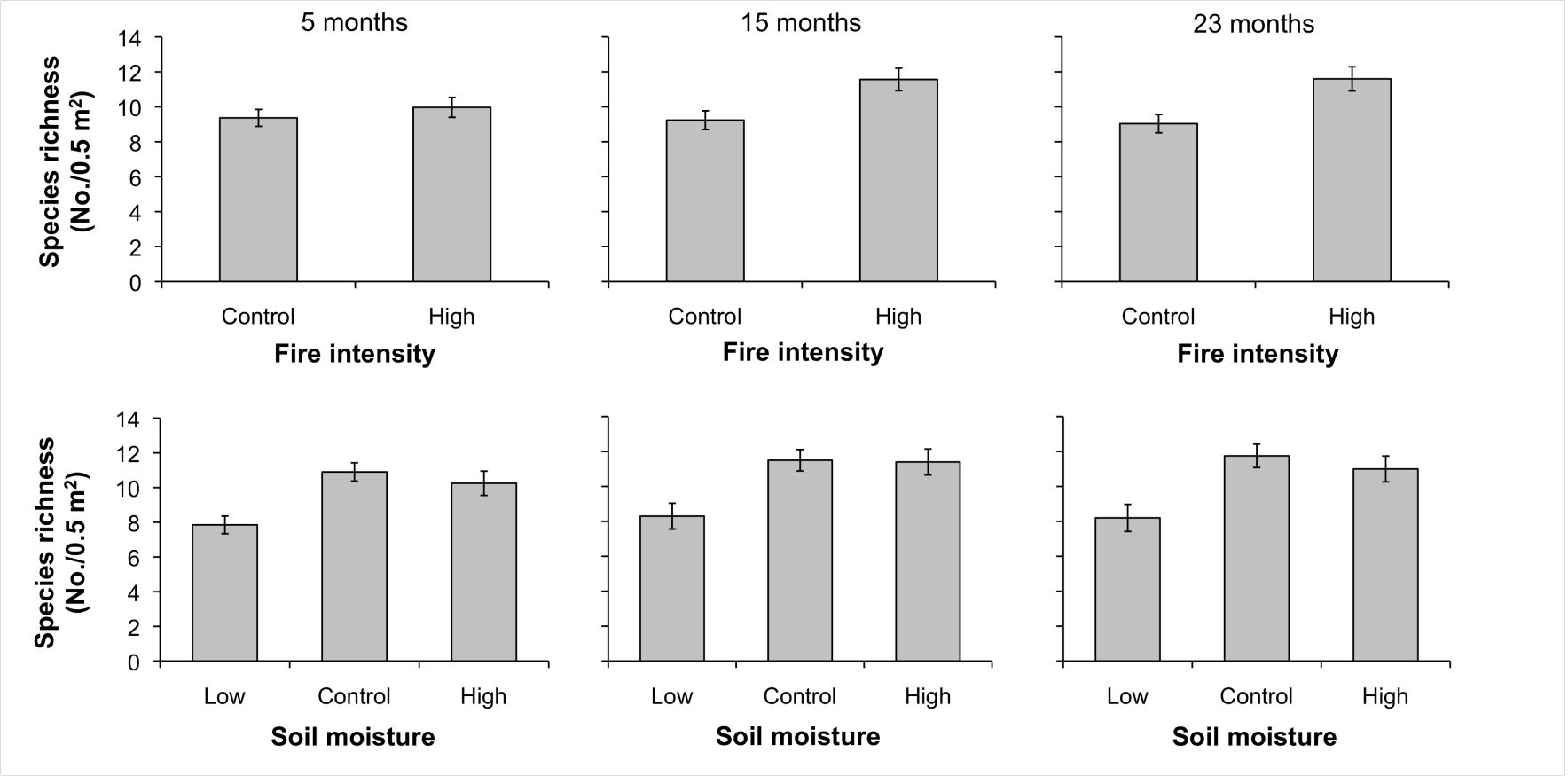
Results from mixed-effects ANOVA testing for effects of fire intensity and soil moisture on total aboveground plant biomass in Fall 2007 and soil volumetric water content (soil moisture) in Summer 2008. Soil water was analyzed at two depths (7.5 and 20 cm). *P* values <0.05 are indicated in bold.

Variable	DF	denDF	F	*P*
Total biomass/0.25 m^2				
Fire intensity	1	53	21.01	**<0.0001**
Soil moisture	2	53	7.70	**0.0012**
Fire intensity x Soil moisture	2	53	0.54	0.5850
Soil moisture				
Fire intensity	1	53	0.16	0.6839
Soil moisture	2	53	586.32	**<0.0001**
Depth	1	54	109.03	**<0.0001**
Fire intensity x Soil moisture	2	53	0.75	0.4752
Fire intensity x Depth	1	54	0.77	0.3840
Soil moisture x Depth	2	54	97.91	**<0.0001**
Fire intensity x Soil moisture x Depth	2	54	1.25	0.2936

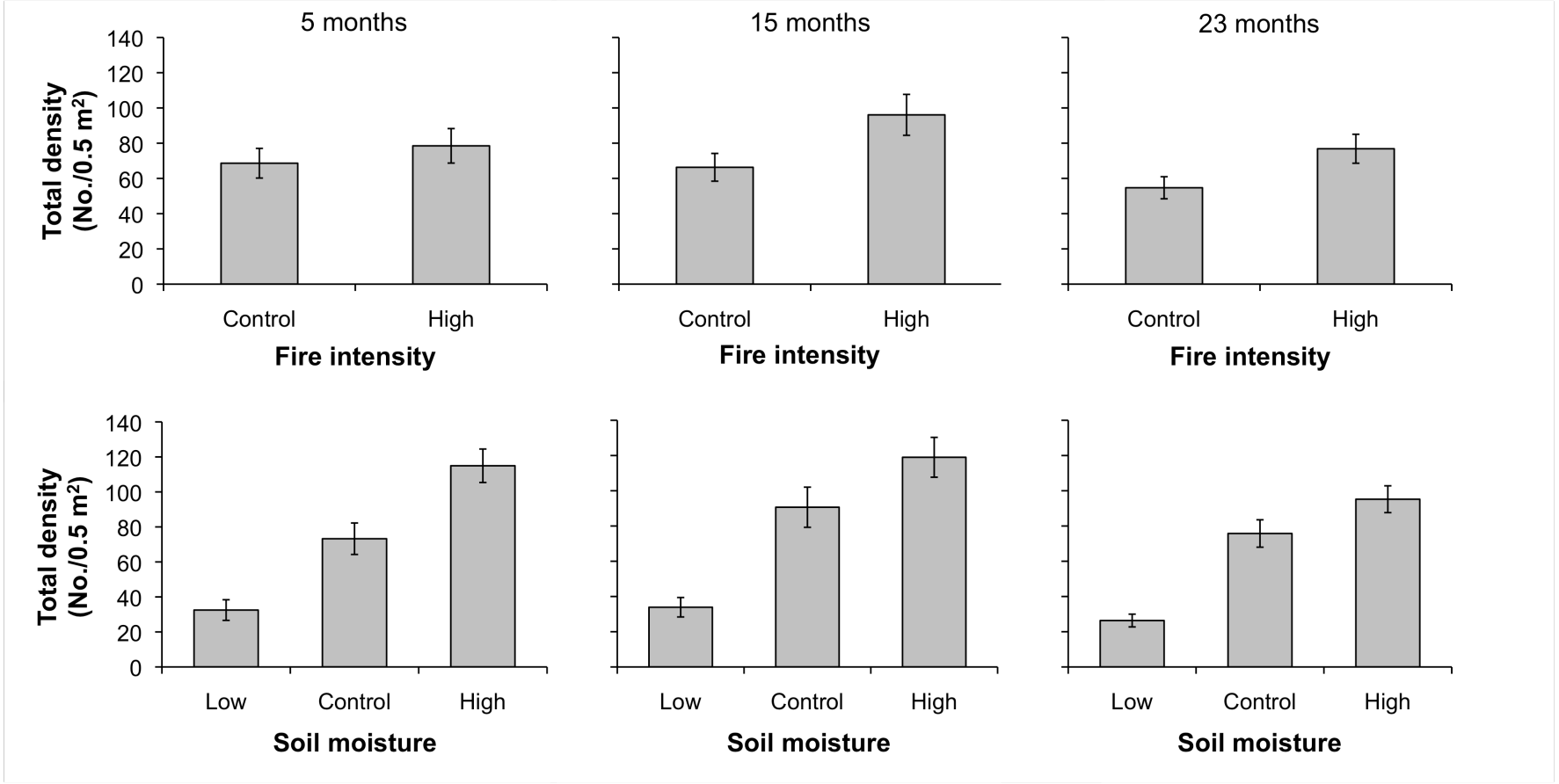
Results from mixed-effects ANOVA testing for effects of fire intensity, soil moisture, dispersal (seed addition), and time on total species richness, seed-addition species richness, and total density of seed-addition species. Seed-addition species richness and density were analyzed using data only from seed-addition subplots because seed-addition species occurred infrequently in seed-control subplots. Seed-addition species richness was square-root transformed and total density was $\log_{10}$-transformed to normalize residuals. *P* values <0.05 are indicated in bold.

Variable	DF	denDF	F	*P*
Total species richness				
Fire intensity	1	53	13.22	**0.0006**
Soil moisture	2	53	4.99	**0.0103**
Dispersal	1	54	144.74	**<0.0001**
Time	1	220	16.50	**<0.0001**
Fire intensity x Soil moisture	1	53	1.84	0.1674
Fire intensity x Dispersal	2	54	10.65	**0.0019**
Fire intensity x Time	2	220	45.20	**<0.0001**
Soil moisture x Dispersal	2	54	4.01	**0.0238**
Soil moisture x Time	4	220	1.67	0.1566
Dispersal x Time	2	220	0.99	0.3721
Fire intensity x Soil moisture x Dispersal	2	54	0.44	0.6442
Fire intensity x Soil moisture x Time	4	220	1.37	0.2446
Fire intensity x Dispersal x Time	2	220	0.18	0.8316
Soil moisture x Dispersal x Time	4	220	1.24	0.2914
Seed-addition species richness				
Fire intensity	1	53	6.75	**0.0121**
Soil moisture	2	53	9.75	**0.0002**
Time	2	108	3.55	**0.0319**
Fire intensity x Soil moisture	2	53	0.62	0.5393
Fire intensity x Time	2	108	5.35	**0.0060**
Soil moisture x Time	4	108	0.48	0.7447
Fire intensity x Soil moisture x Time	4	108	0.25	0.9041
Total density of seed-addition species				
Fire intensity	1	53	3.55	0.0650
Soil moisture	2	53	42.91	**<0.0001**
Time	2	108	9.03	**0.0002**
Fire intensity x Soil moisture	2	53	0.15	0.8582
Fire intensity x Time	2	108	3.98	**0.0214**
Soil moisture x Time	4	108	1.46	0.2186
Fire intensity x Soil moisture x Time	4	108	0.18	0.9452

Richness and Total Density of Seed-addition Species



Richness of seed-addition species in the fire-intensity and soil-moisture treatments 5, 15, and 23 months post fire. Bars = means ± 1 SE; n = 30 (fire intensity) and 20 (soil moisture) subplots. Results are shown for the high-dispersal (seed addition) treatment; most species were absent or rare in the low-dispersal (control) treatment.



Total density of seed-addition species in the fire-intensity and soil-moisture treatments 5, 15, and 23 months post fire. Bars = means ± 1 SE; *n* = 30 (fire intensity) and 20 (soil moisture) subplots. Results are shown for the high-dispersal (seed addition) treatment; most species were absent or rare in the low-dispersal (control) treatment.

APPENDIX B. SUPPLEMENTARY MATERIAL FOR CHAPTER 3

Species, Densities, and Viability of Seeds Used in the Immigration Treatment

Thirty-eight focal species added in the immigration treatments in 2006 and 2007, showing their dispersal type based on seed morphology, number of seeds added per plot in each year, and percent seed germination on petri dishes for 2007 seeds (n = 50 seeds/species).

Species	Family	Life form[1]	Disp type[2]	*n* seeds added/plot		Germ (%)
				2006	2007	
Ageratina aromatica	Asteraceae	PF	W	–	150	94
Asclepias sp.	Asclepiadaceae	PF	W	10	–	–
Carex glaucescens	Cyperaceae	PS	G	20	–	–
C. tenax	Cyperaceae	PS	G	–	30	94
Chromolaena ivifolia	Asteraceae	PF	W	–	150	68
Chrysopsis mariana	Asteraceae	PF	W	–	30	26
Cirsium horridulum	Asteraceae	BF	W	–	40	88
Conoclinium coelestinum	Asteraceae	PF	W	–	200	96
Crotalaria purshii	Fabaceae	PL	G	–	50	14
Elephantopus tomentosus	Asteraceae	PF	W	200	300	88
Eryngium yuccifolium	Apiaceae	PF	G	–	50	30
Eupatorium rotundifolium	Asteraceae	PF	W	300	100	40
Eurybia paludosa	Asteraceae	PF	W	–	30	26
Helenium flexuosum	Asteraceae	PF	G	25	50	88
Helianthus angustifolius	Asteraceae	PF	G	–	100	78
H. hirsutus	Asteraceae	PF	G	5	–	–
H. radula	Asteraceae	PF	G	–	100	76
Hibiscus aculeatus	Malvaceae	PF	G	35	–	–
Hieracium gronovii	Asteraceae	PF	W	40	–	–
Hypericum crux-andreae	Clusiaceae	PW	G	–	50	46
H. setosum	Clusiaceae	PF	G	–	200	88
Hyptis alata	Lamiaceae	PF	G	50	200	54
Lespedeza capitata	Fabaceae	PL	C	–	30	4
Liatris pycnostachya	Asteraceae	PF	W	–	30	28
L. squarrulosa	Asteraceae	PF	W	–	30	66
Ludwigia hirtella	Onagraceae	PF	G	150	100	82
Nothoscordum bivalve	Liliaceae	PF	G	15	–	–
Orbexilum pedunculatum	Fabaceae	PL	G	10	–	–
Pityopsis graminifolia	Asteraceae	PF	W	–	30	30
Plantago virginica	Plantaginaceae	AF	G	–	30	98
Pycnanthemum albescens	Lamiaceae	PF	G	–	300	16
P. tenuifolium	Lamiaceae	PF	G	20	–	–
Rhexia alifanus	Melastomataceae	PF	G	30	30	14
Rhynchosia reniformis	Fabaceae	PL	B	–	5	48
Rudbeckia hirta	Asteraceae	PF	G	300	50	30
Salvia lyrata	Lamiaceae	PF	G	–	30	62
Solidago odora	Asteraceae	PF	W	–	100	84

S. rugosa	Asteraceae	PF	W	–	400	36

[1]A = annual, B = biennial, F = non-legume forb, L = legume forb, S = sedge, W = woody
[2] B = ballistic, C = carried, G = gravity, W = wind

ANOVA Table for Species Richness

Results from ANOVA testing fixed effects of immigration, competition, and their interaction (Imm x Com) on total species richness (0.01 and 0.25 m^2) and focal species richness (0.25 m^2) in the bunchgrass and shrub experiments in 2007 and 2008.

Variable	Bunchgrass experiment					Shrub experiment				
		2007		2008			2007		2008	
	df	F	*P*	F	*P*	df	F	*P*	F	*P*
Total richness (0.25 m^2)										
Immigration	1	51.82	<0.0001	86.23	<0.0001	1	21.62	0.0001	58.04	<0.0001
Competition	2	0.50	<0.6049	1.23	0.2995	1	4.71	0.0390	21.41	0.0001
Imm x Com	2	0.36	0.6955	0.70	0.5016	1	2.09	0.1595	1.83	0.1865
	59					39				
Total richness (0.01 m^2)										
Immigration	1	10.18	0.0026	29.58	<0.0001	1	2.64	0.0112	18.12	0.0002
Competition	2	0.66	0.5189	4.81	0.0127	1	7.41	0.1155	31.93	<0.0001
Imm x Com	2	0.42	0.6532	0.40	0.6683	1	3.52	0.0711	1.18	0.2861
	59					39				
Focal richness (0.25 m^2)										
Immigration	1	140.17	<0.0001	252.45	<0.0001	1	121.60	<0.0001	260.01	<0.0001
Competition	2	0.01	0.9851	0.90	0.4131	1	0.04	0.8360	7.99	<0.0087
Imm x Com	2	1.35	0.2680	3.33	0.0446	1	2.29	0.1418	0.82	0.3728
	59					39				

Plot Occupancy and Mean Density of Seed-addition Species

Plot occupancy (%) and mean plant density/m^2 of the 38 focal seed-addition species in the immigration treatments (Con = control, Inc = increase) in the bunchgrass and shrub experiments in 2008. Plot occupancy indicates the percentage of all plots in which a species was present (n = 30 and 20 plots/treatment for the bunchgrass and shrub experiment, respectively). Observed maximum natural densities of focal species present in 60 0.5-m^2 plots sampled in 2007 and 2008 in a separate, concurrent study at the field site (J.A. Myers and K.E. Harms, unpublished data) is shown for comparison against densities observed in the experimental seed-addition plots in the current study.

Species	Plot occupancy (%)				Plant density/m^2				Max. obs. density/m^2
	Bunchgrass		Shrub		Bunchgrass		Shrub		
	Con	Inc	Con	Inc	Con	Inc	Con	Inc	
Ageratina aromatica	0	3	0	0	0	0.1	0	0	38
Asclepias sp.	0	27	0	40	0	1.2	0	0.2	–
Carex glaucescens	0	0	0	0	0	0	0	0	–
C. tenax	0	0	0	0	0	0	0	0	–
Chromolaena ivifolia	0	0	0	0	0	0	0	0	–
Chrysopsis mariana	3	10	0	0	0.1	0.9	0	0	4*
Cirsium horridulum	3	77	30	85	0.1	8.9	0	9.0	6
Conoclinium coelestinum	0	0	0	0	0	0	0	0	–
Crotalaria purshii	0	27	0	40	0	1.6	0	0.2	–
Elephantopus tomentosus	7	100	0	90	0.4	51.6	0	52.6	66
Eryngium yuccifolium	7	13	5	40	0.4	0.7	0	0	–
Eupatorium rotundifolium	33	60	10	55	3.7	5.1	1.6	3.2	64
Eurybia paludosa	13	17	10	35	0.9	1.9	0	0.6	4
Helenium flexuosum	0	10	0	0	0	0.7	0	0	–
Helianthus angustifolius	7	40	0	20	0.5	3.3	0.4	2.2	38*
H. hirsutus	0	0	0	15	0	0	0	0.2	–
H. radula	27	90	0	40	6.0	33.9	0	15.0	214
Hibiscus aculeatus	0	57	5	55	0	4.4	0	2.8	34*
Hieracium gronovii	0	3	0	0	0	0.3	0	0	4
Hypericum crux-andreae	7	17	0	0	0.2	1.9	0	0.6	8*
H. setosum	10	3	0	5	0.8	0.1	0	0.2	–
Hyptis alata	0	47	5	30	0	5.9	0.4	11.8	–

Lespedeza capitata	0	0	0	0	0	0	0	0	–
Liatris pycnostachya	0	0	0	0	0	0	0	0	–
L. squarrulosa	0	3	0	0	0	0.1	0	0	4
Ludwigia hirtella	0	30	0	10	0	2.9	0	1.2	2
Nothoscordum bivalve	0	0	0	0	0	0	0	0	–
Orbexilum pedunculatum	0	0	0	0	0	0	0	0	–
Pityopsis graminifolia	73	57	10	10	10.0	10.4	1.4	1.4	38*
Plantago virginica	0	83	0	25	0	10.5	0	13.6	–
Pycnanthemum albescens	0	20	0	15	0	0.8	0	0.6	4
P. tenuifolium	0	0	0	0	0	0	0	0	–
Rhexia alifanus	0	13	0	5	0	0.7	0	0.2	–
Rhynchosia reniformis	0	3	0	0	0	0.1	0	0	–
Rudbeckia hirta	0	63	0	30	0	6.5	0.2	6.0	8
Salvia lyrata	0	50	0	30	0	5.5	0	4.4	–
Solidago odora	90	93	15	45	18.8	23.2	4.0	16.2	360
S. rugosa	0	87	0	45	0	19.9	0	9.6	18

*Max. observed density estimated conservatively using presence/absence of species in 0.01-m^2 grid cells

APPENDIX C. SUPPLEMENTARY MATERIAL FOR CHAPTER 4

Homogeneity statistics and *P*-values from categorical and continuous mixed-effects models. The results are summarized in Figure 4.1 (categorical models) and Figure 4.2 (continuous models). df = degrees of freedom, Q_B = between-class homogeneity, Q_W = within-class homogeneity, *P* = level of significance for Q_B (*P*-values <0.05 are shown in bold).

Variable	df_{total}	Q_B	Q_W	*P*
Categorical				
Disturbance	39	5.96	48.51	**0.0145**
Nutrient	7	1.17	6.97	0.2785
Water	7	0.03	6.42	0.8420
Continuous: No disturbance				
Species richness	16	0.83	20.80	0.3621
Species evenness	16	4.78	18.12	**0.0287**
Functional richness	16	1.50	19.74	0.2201
Functional evenness	16	1.12	18.97	0.2887
Seed size diversity	16	0.21	21.02	0.6431
Continuous: Disturbance				
Species richness	17	0.003	19.14	0.9553
Species evenness	17	13.27	16.00	**0.0002**
Functional richness	17	0.42	18.85	0.5136
Functional evenness	17	3.10	16.74	0.0779
Seed size diversity	17	7.68	17.03	**0.0055**

APPENDIX D. LETTERS OF PERMISSION

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VITA

Jonathan Andrew Myers was born in February 1979, in Lockport, New York. His interest in the natural world was piqued by his early outdoor experiences in the forests and fields of western New York. In high school, Jonathan completed a 2-year vocational program in natural resources conservation, which sparked his interest in a career in the natural sciences. In May of 1999, Jonathan received an associate's degree from Paul Smith's College in Paul Smiths, New York, with a major in forest recreation. During his time at Paul Smith's, he participated in a tropical ecology field course in Belize, which stimulated his interest in tropical biology, and worked as a botanist in the Adirondacks for the United States Forest Service. In May of 2002, Jonathan received a bachelor's degree from Cornell University in Ithaca, New York, with a major in biological sciences and a concentration in ecology and evolutionary biology. While at Cornell, he completed an honors thesis on seed dispersal by white-tailed deer under the supervision of Peter Marks, as well as a research internship in tropical ecology at the Smithsonian Tropical Research Institute in Panama. After graduation, he worked as a research assistant for the Institute of Ecosystem Studies at the Luquillo Experimental Forest in Puerto Rico. In August 2002, Jonathan joined the Department of Botany at the University of Florida in Gainesville, Florida, as a master's student in Kaoru Kitajima's research group. His thesis research explored eco-physiological mechanisms influencing the shade and stress tolerance of seedlings in a tropical forest in Panama. In January 2005, he joined the Department of Biological Sciences at Louisiana State University in Baton Rouge, Louisiana, as a doctoral student in Kyle Harms' research group. His dissertation research examined ecological mechanisms influencing community assembly and the maintenance of biodiversity in species-rich longleaf pine savannas of the southeastern United States. In May 2010, Jonathan will begin a postdoctoral fellowship in the Department of Biology at Washington University in St. Louis, Missouri.